Salmon population in watersheds of different complexities following ice recession in Glacier Bay as determined by the physical habitat template

by

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Abstract

Colonization and successional change over time is important in the understanding of landscape evolution. Glacier Bay, southeast Alaska is unique, as vegetation and invertebrate colonization and succession can be studied *in-situ* using a chronosequence approach. The diets of sympatric stream dwelling juvenile coho salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*) were analyzed in five streams of different age since glacial retreat in Glacier Bay. Interferometric synthetic aperture radar (IFSAR) data were analyzed with geographic information systems (GRASS GIS) to understand watershed change since deglaciation. Spatiotemporal variations of watershed characteristics from GIS were then used to develop a four-dimensional physical habitat template (PHT) and a directional model of stream development. Juvenile coho salmon and Dolly Varden coexisted in all streams with a strong overlap in diet while using different foraging zones. Diet niche breadth for both species increased with the amount of terrestrial insects in the diet as a result of resource depression, as mean fork length (FL) of juvenile fish increased when aquatic insects were a greater part of the diet, but decreased with greater terrestrial input. Using stable isotopes $\delta^{15}N$ and $\delta^{13}C$, the contribution of marine derived nutrients (MDN) to stream biota was determined by salmon spawner abundance and watershed retention, and an increase in $\delta^{15}N$ and $\delta^{13}C$ dispersion (SD) was found with stream age, likely causing a difference in the fractioning of $\delta^{15}N$ and $\delta^{13}C$. The most significant change with stream age was denudation of watersheds and the development of stream networks. Dietary overlap was linked to fish resource depression, and found to be controlled by stream geomorphology. Sea lice (*Lepeophtheirus salmonis)* were found to make a major contribution to the diet of juvenile salmonids in the older streams, but not in the younger streams, due to lower salinity in the upper part of the fjord from glacial freshwater runoff. Findings in this study indicates that sustainability of juvenile fish population communities within the watersheds PHT are more influenced by abiotic factors, notably geomorphological changes within the watersheds. Initial PHT controls the watershed development and provides an understanding of temporal change.

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1.1 Introduction

Glacial recession in Glacier Bay National Park in southeast Alaska uncovers post-glacial landforms providing a unique opportunity to study geomorphological and biological transitional changes over time thereby providing insights into ecosystems response to the interaction of landscape, climate, and biotic variables (Kling 2000). Crucial to the understanding of ecosystems on several temporal and spatial scales is to understand the form, behavior, and historical context of landscapes (Swanson et al. 1988). The chronosequence is a tool for studying space-for-time changes in earth surface systems (Phillips 2015), and in Glacier Bay the chronosequence of 250 years provides the opportunity to study landscapes within a relatively small temporal scale. The development of the ecosystem is initially dominated by physical processes but with time biotic drivers become more important (Milner et al. 2007). The rapid increase in plant communities richness during the first 100 years in Glacier Bay (Reiners et al. 1971), and the rapid establishment of salmonids and invertebrate communities across entire watersheds over time influences the development of biodiversity (Milner et al. 2000, 2011). Sidle and Milner (1989) found the amount of suitable fish habitat increases as postglacial stream developed, with greater percent pools and riparian cover and decreasing sediment transport. Development of larger vegetation increase the input of larger coarse woody debris (CWD), and older streams support significantly greater abundance of microcrustacean and macroinvertebrates taxa as well as juvenile fish abundance and diversity (Milner et al. 2000). This development is related to the geomorphic history of the watershed which influence distribution of aquatic habitat and organisms (McKean et al. 2008).

Landscape evolution and morphological parameters of the watersheds are important to understand ecological community development after colonization in both terrestrial and

aquatic environments. Wipfli and Gregovich (2002) emphasized that transport of energy (prey and detritus) from one ecosystem area could subsidize both proximal and distant food webs, which again usually increase primary and secondary productivity, both directly and indirectly (Polis et al. 1997). Critical resources can be provided to organisms in receiving habitats by spatial subsidies, influencing population and community dynamics (Wilson et al. 2014). Fish behavior should alter in response to low food availability to ensure higher feeding rates, larger territories, and broader diet (Dill 1983). Juvenile coho salmon and Dolly Varden are present in all study streams, and (Milner and Bailey 1989) found juvenile Dolly Varden to be more abundant in recently formed clearwater streams, due to the characteristic absence of pool habitat. Nakano and Kaeriyama (1995) found juvenile coho salmon to be typical drift feeders holding focal point in the mid water column, while juvenile Dolly Varden intercepted drifting prey with focal point near the stream bed, and frequently selected benthic invertebrates from the substrate, and found overlap between juvenile coho salmon and Dolly Varden diet. Ecosystem subsidies of energy, nutrients and material cross ecosystem boundaries can affect consumer abundance and are well established, however there is less information available on how subsidies may affect consumer species diet, body condition and trophic position (Briggs et al. 2012). Wipfli (2005) illustrated that headwaters are source areas for aquatic and terrestrial invertebrates and detritus, but ecological links between headwater streams and larger stream orders downstream are poorly documented (Wipfli et al. 2007). Up to half of the annual energy budget to drift-feeding salmonids could be contributed by terrestrial invertebrate fluxes (Baxter et al. 2005). However little information is available on wether changes in vegetation structure commonly associated with spatial variation in subsidies may play a role in the response of the consumer to these subsidies (Briggs et al. 2012). While resource subsidies studies have emerged as key topics in both ecosystem and food web ecology, the discussion has been limited in regard to their role due to separate approaches that emphasize either subsidy quantity or quality (Marcarelli et al. 2011). Loreau et al. (2003) proposed a meta-ecosystem concept, defined as a set of ecosystems connected by spatial flows of energy, materials and organisms across ecosystems boundaries. An understanding of

variation in juvenile salmonid survival and growth on a watershed scale can give us insights into factors influencing demographics (Ebersole et al. 2006), and study of reciprocal prey linkages help to define a more holistic perspective of catchments (Baxter et al. 2005). Glacier Bay provides a great opportunity to create a more holistic perspective, and can provide information in relation to how subsidies may affect juvenile salmonids diet, growth and abundance with watershed age and complexities.

Colonization by Pacific salmonids influences watersheds by contributing marine derived nutrients (MDN) upon their return to spawn in their natal stream. Large transfers of MDN from Pacific salmon to adjacent forest ecosystems have a profound effect on plant and wildlife production (Merz and Moyle 2006), and helps sustain the productivity of freshwater food webs (Chaloner and Wipfli 2002). MDN enhances riparian production, which again might serve as a feedback mechanism to increase spawning and rearing habitats for subsequent salmon generations (Helfield and Naiman 2001). Juvenile coho salmon fork lengths and weights have been found to significantly increase with the addition of salmon carcasses (Wipfli et al. 2003), and condition factor increase (Bilby et al. 1998). The influence of marine derive nutrients (MDN) on watersheds ecology is now widely acknowledged and recognized as important (Levy 1997, Cederholm et al. 1999), despite this MDN subsidy into fish trophic ecology remains poorly understood (Scheuerell et al. 2007) especially as streams develop over time. Quantities of spawning salmonids are known to influence the quantity of MDN delivered, but the mechanism behind nutrient delivery is little known (Rex and Petticrew 2008). A wide range of results of biota abundance increase and decrease due to MDN contribution, and (Kiffney et al. 2014) found a strong bottom-up effect on selected invertebrates. But the mechanisms causing the wide ranging in results have not been addressed (Tiegs et al. 2009). This potential increase in ecosystem productivity (Fellman et al. 2008), will influence the development of the watersheds. There are still some discordant views regarding their ecological effects (Rex et al. 2014), much of which could be contributed to the lack of an overall knowledge of the cocktail effect of salmon spawners and watersheds

interacting together on MDN distribution and availability. The distribution and retention with watershed age in Glacier Bay can provide information on the ecologic effect and the mechanism behind nutrient delivery due to difference in time since colonization.

Spatial patterning and geographic distribution of organisms has long been of interest to ecologists (Turner 1989). Characteristics of ecological systems at relatively fine scales differ from those at relatively broad scales (Wiens 1989). Using the watershed as scale provide a frame for studying the development and the colonization and succession of vegetation and macroinvertebrates, as well as the dynamics and across habitats and environments within. Variables and processes within hydrology usually exhibit a large spatial variability, often including organization and randomness (Merz and Plate 1997). Impact of geomorphology on succession and change on a watershed scale will affect the time of colonization, and successional processes. Landscape ecology is well integrated in ecology (Turner 2005), but little attention has been dedicated to the specter of landform effects in landscape ecology literature (Swanson et al. 1988). So far, few empirical studies have assessed how regional, dispersal-related processes and local habitat factors interact to control network patterns of species composition (Kuglerová et al. 2015). Arguably, one central issue in ecology has been the problem of pattern and scale (Levin 1992). To detection of the different disturbance effects on a given biological response value require both appropriate spatial and temporal scales (Poff and Ward 1990). By applying a broad spatiotemporal perspective, the dynamics of pristine lotic ecosystems can be therefore be understood (Ward 1989), who conceptualized a four dimensional framework consisting of a lateral, longitudinal, vertical and temporal scale. By using what (Minkowski 1908) formulated as a "Weltpunkt", a point in space and time (x,y,z,t) creating a four dimensional system, a watershed physical habitat template (PHT) can be created. Species and communities flow, interact, and evolve through a continuum of time (Rull 2014), and can this way be addressed. Habitat as a template for ecological strategies was presented by (Southwood 1977), and made up of a continuum of habitat heterogeneity, employing space and time as two basic dimensions. History of physicochemical variability

and complexity and stability of the substratum establishes therefore a physical habitat template (Poff and Ward 1990). Southwood's habitat templet is suitable for development of hypotheses and the ordering of knowledge along spatiotemporal axes (Minshall 1988).

The spatial and temporal scales of study are important factors in analyzing and understanding patterns and processes in biology, geology, hydrology and chemistry, where the scale of investigation determine the range of patterns and processes that can be detected (Wiens 1989). One of the most powerful methods to map abiotic and biotic components of ecosystems and estimate their change over time is remote sensing (Rocchini et al. 2013). Morphological information can be derived with software tools from digital elevation models (DEMs) (Jenson and Domingue 1988). Development in aerial and satellite imaging can increase the accuracy of geographic information systems (GIS) analysis on a smaller scale, and can help us understand the different interactions between environments and across their boundaries. Long-term studies are needed to understand ecological dynamics, while widely recognized it has not satisfactorily been addressed to date (Rull 2014). Understanding the interconnectedness and the interacting processes between and among environments will both allow for better modeling and understanding how species and environment interact as a whole. The development sequence of landforms is in its own way as systematic as sequences found in development of organic forms (Davis 1899). All processes are factors in an ever changing landscape, regardless of rapid turnovers or not. The importance of chaos (deterministic complexity) where the «initial» state control the colonization and succession in watersheds after deglaciation, and provides insight in these two processes, impacting the direction of change in ecosystems. This research investigated the contribution of spawning salmonids and diet of juvenile coho salmon and Dolly Varden. When analyzed together with watershed characteristics this provide an understanding of cross boundary nutrient flow on a larger scale, and in turn the “landscapes of salmonids”.

1.2 Aim and objectives

The aim of the research was to assess the diets of juvenile coho salmon and Dolly Varden as how these change with watershed stream development after glacial retreat in Glacier Bay, southeast Alaska.

By addressing research gaps and achieving the aim of the project, the objectives of the study were;

1. Create a physical habitat template (PHT) based on morphologic factors of watersheds across a temporal scale using GIS (Chapter 2) to inform the principal drivers of juvenile salmon populations in watersheds of different ages.

2. Describe the in-stream diet of juvenile coho salmon and Dolly Varden and their niche breadth and overlap in a series of different aged streams across a chronosequence in Glacier Bay to ascertain if there is and changes with stream development (Chapter 3 and 5).

3. Assess the contribution of nutrients from the marine environment through the colonization and life cycle of Pacific salmonids to the stream food web and juvenile fish populations (Chapter 4).

4. Examine how quantifying the physical habitat template within watersheds elucidate the interconnectedness between biota and landscape as watersheds change over time (Chapter 6).

1.3 Thesis structure

This thesis was written as a series of paper drafts with a brief contextual introduction with background information for each chapter and a summary elucidation the interconnectedness of the watershed physical habitat and biota, both spatially and temporally.

Chapter 1: Introduction. This chapter provides a brief background on Glacier Bay and stream dwelling juvenile coho salmon and Dolly Varden, and MDN from returning salmon. The spatial and temporal effects on landscapes and ecological dynamics.

Chapter 2: The application of geographic information systems (GIS) to characterize the spatiotemporal dynamics of the physical habitat template in rivers at a watershed scale. This chapter develops a physical habitat template (PHT) in a four dimensional space, and a directional development model PHT, based on interferometric synthetic aperture radar (IFSAR) data of the studied watershed streams in Glacier Bay with the help of GIS.

Chapter 3: Diet of juvenile coho salmon and Dolly Varden in streams of different age since deglaciation in Glacier Bay National Park, Alaska. This chapter examines the diet of juvenile coho salmon and Dolly Varden, which have colonized the study streams. Diet niche breadth and diet overlap with stream age were analyzed, and the proportion of diet derived from aquatic-, terrestrial- and marine environment sources is examined.

Chapter 4: Influence of marine derived nutrients in streams of different catchment age. This chapter explores the influence of MDN by spawning salmonids on watersheds of different age by analyzing isotopic $\delta^{15}N$ and $\delta^{13}C$ measurements.

Chapter 5: Sea lice (Lepeophtheirus salmonis) as a food source for juvenile salmonids in southeast Alaska. This chapter examines the unique findings of sea lice as a food source for

juvenile in-stream salmonids and how their availability changes according to salinity in the fjord close to the estuaries of the study stream.

Chapter 6: Summary. This chapter synthesis the finding of chapters 2 to 5 to illustrate the interconnectedness of landscape and biota, and how the "initial" PHT determine future development in time and space of the watersheds and the juvenile fish populations.

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2: The application of GIS to characterize the spatiotemporal dynamics of the physical habitat template in rivers at a watershed scale.

Abstract

To understand river systems and their development one has to characterize spatial and temporal processes within their watersheds. Watersheds in Glacier Bay, southeast Alaska, have developed after glacial retreat since the Little Ice Age (LIA). Basic physical morphological features of five watersheds of different ages after deglaciation in Glacier Bay were analyzed using interferometric synthetic aperture radar (IFSAR) and geographic information systems (GRASS GIS). Based on the physical morphological features, the initial state after glacial retreat and the location of the watershed seemed to determine the temporal effect and successional processes. Initial topology was the main driver in watershed development. Mean watershed slope negatively influenced drainage density significantly ($p<0.05$) and had a negative impact on vegetation cover. Morphological differences also indicated a difference in infiltration among the watersheds, which most likely are caused by larger glacial sediment depositions. Vegetation cover influenced drainage density, and the number of streams within watersheds, due to development of top soil caused by litter fall, and thereby increased the stream network. Watershed age significantly correlated with the total number of streams ($p<0.05$) and was the best indicator of watershed development in Glacier Bay. The mosaic of physical habitat variation in the watershed is connected by a stream network, whereas the heterogeneous habitats they create influences the biotic community. A conceptual model of how to create a physical habitat template (PHT), and describing its directional development, is here presented to further understand stream development and knowledge of watershed analysis. The directional development model is based on combining three-dimensional variables at time t to provide a PHT at a point in time. With a temporally continuous PHT, postglacial processes can as a result be assessed within the given PHT. GIS

can therefore be a tool to better understand how stream environments and habitats function as a whole, and provide information on how development affects stream communities. Determining a four-dimensional PHT on a watershed scale will help us understand the interconnectedness within a stream network and its watershed, providing a more holistic view of connectivity and landscape processes. The PHT framework provided here will contribute to management, modeling and biological studies.

2.1 Introduction

2.1.1 Physical habitat template (PHT) of a riverscape

The living space of the stream biota is the physical habitat, a spatially and temporally dynamic entity (Maddock 1999). To understand streams and their development several concepts have been created; the river continuum concept (Vannote et al. 1980), the concept of a hyporheic corridor (Stanford and Ward 1993) and the discontinuum concept (Ward and Stanford 1983). The Flood pulse concept (Junk et al. 1989) takes it one step further to understand processes and patterns within a watershed. The continuum of the biosphere (Rull 2014) however gives that everything is interconnected through time. Streams are strong hierarchical and patchy systems (Poole 2002), and the outside and inside of the stream are interconnected, creating a mosaic of habitats. Southwood (1977) presented the habitat as a template for ecological strategies, consisting of a continuum of habitat heterogeneity, using space and time as two basic dimensions. Ward (1989) conceptualized the dynamical hierarchical nature of lotic ecosystems into a four-dimensional framework, consisting of longitudinal, lateral, vertical and time, since lotic ecosystems are open systems and in effect highly interactive with their surroundings. By the use of remote sensing and geographic information systems (GIS), a framework for a general physical habitat template (PHT) can be developed (Figure 2.1). Minkowski space (Minkowski 1908) is used to describe an integration of a four-dimensional point/resolution layer system (x,y,z,t) that will create a three dimensional structural physical habitat template at a point in time. Storing the temporal component in the geometry of space-time (Hazelton et al. 1990).

Ferrari and Ferrarini (2008) concluded that ecosystem and landscape ecology differ from a theoretical viewpoint, due to the difference in spatial and temporal scales used. Watersheds give natural boundaries to the stream systems, and the heterogeneity within create a PHT as a platform for studies of riverscapes. By using a common PHT framework as a platform which

sets the scale, the temporal effect will be varying depending on the initial PHT space. The larger the scale of the PHT, the higher the demand will be for increased resolution. Since the resolution will determine the rate of change that can be observed, this will vary on a spatial scale and on the initial state of the PHT. The facilitating factors of watersheds, like morphology, climate and watershed location influence and control both colonization and succession of the watershed. This integrated approach can describe all the variables that are measured within a defined scale, which is her set to the size of a watershed, which change through time. Using a PHT as a background for ecological interactions makes it easier to understand population colonization, migration and interactions.

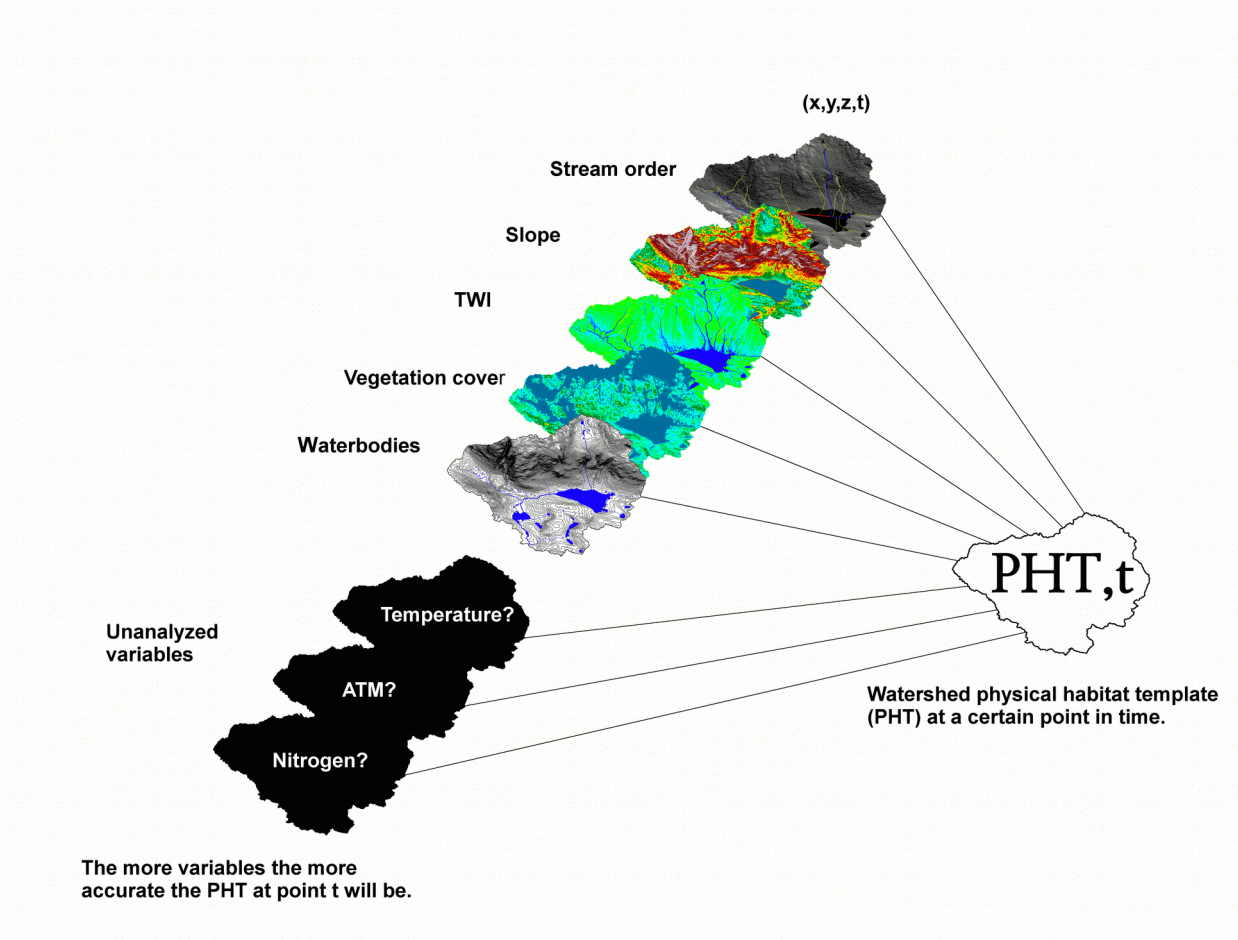

Figure 2.1: Framework for a remote sensed physical habitat template, PHT.

2.1.2 Scale and resolution

Riverscapes are dynamic environments, and scale and resolution are the two main factors controlling how and if development processes are detectable. Terrestrial and aquatic complexities within the watershed are integrated, and tools to seamlessly map both domains will therefore be required to fully understand these systems (McKean et al. 2008). When mapping on a watershed scale, biota and nutrient transfer can more readily and more accurately be assessed, without extrapolation from reach sections. The stream functions like "blood vessels" into the landscapes, bringing nutrients downstream and out to the ocean, while making a conduit for fish, insects and animals upstream. Nutrients, material and biota can also use rain, wind and other biological conduits for looping upstream. All these interactions create a mosaic of habitats within the landscape.

Frissell et al. (1986) developed a hierarchal classification system to view stream habitats in the context of the watershed. Spatial scales within the watershed can together with increasingly accurate remote sensing, contribute to connect Frissel's classification system together with a continuous spatiotemporal watershed and the heterogeneous habitats present within. This would allow better understanding of the sampling sites and the difference between the watersheds, without having to extrapolate. Digital terrain model (DTM) raster is here shown as a two dimensional cell volume system in a modified Frissell et al. (1986) hierarchal classification system (Figure 2.2), with the same resolution at different scales, visualizing how this impact what can be assessed or analyzed.

Representations of spatial and temporal data are controlled by the scale cut-off, of which processes and patterns that can be observed. The influences from surrounding factors are almost infinite and therefore difficult to observe. The importance of scaling will be related to the physical effects they induce on the habitats, and these effects from morphology and geology can originate from around the perimeter of the watershed, and would therefore not be

accounted for on a reach scale (Fausch et al. 2002). Stream delineation in the field would be optimal and would give a much higher resolution of stream network. This is time consuming and in many cases difficult due to almost inaccessible areas. Advances in remote sensing and field equipment implementation of new technologies can now more readily address both scale and resolution. When the watershed scale is used and the satellite data accuracy increases, smaller changes within the watershed can be observed, such as vegetational change, geomorphology and other factors only before described on a reach scale. Temporally yearly fluctuations could be observed if continuously measured.

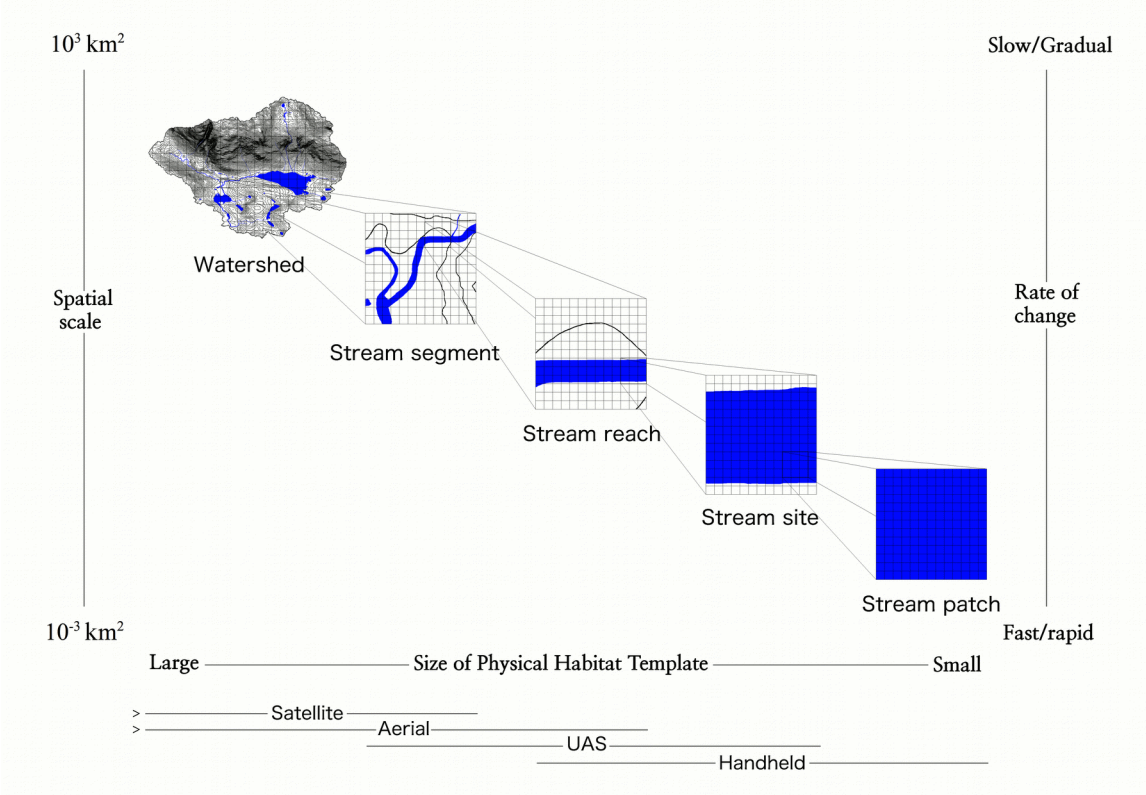

Figure 2.2: Functional classification of a river system based on scale, all with the same DTM raster cell system resolution. (After Frissell et al. 1986, Maddock 1999).

2.1.3 Landscape ecology

Ecologists have mainly studied aquatic and terrestrial ecosystems separately (Soininen et al. 2015), while everything is connected across systems. Historically, selection of habitats for

studies are done with focus on local structures of the environment and mechanisms linked to these local conditions (Keller and Smith 2014). The link between physical habitats and ecological response in rivers are widely recognized, but traditionally poorly quantified (Orr et al. 2008). To understand runoff generation, storm generation, storm hydrology, sediment transport, biogeochemical cycling and landscape evolution, it is fundamental to accurately reconstruct the fluvial domain (Clubb et al. 2014), which gives an ecological understanding of watersheds and the habitats within. Glacial recession in Glacier Bay during the last 250 years has created new watersheds with a spatial and temporal scale. Succession and colonization of vegetation and invertebrates both inside and outside the stream network can therefore be related to the post glacial processes, and it is a unique opportunity to study these processes on a larger spatial scale within a short timeframe. Regulation of material-, organisms-, propagules-, and energy- movement across a landscape is regulated by landforms defining gravitational gradients, flow paths of wind, barriers and corridor formation (Swanson et al. 1988). Understanding watershed responses based on landscape structure is a continuing pursuit for hydrological sciences (Jencso et al. 2010). Morphological features of watersheds are important environmental variables, affecting both colonization and succession in stream and associated ecosystems, and thus processes affected by landforms yield some power in prediction of ecosystem behavior (Swanson et al. 1988). Analyzing and quantifying surface morphology in terms of landform characteristics are essential for understanding of physical, chemical, and biological processes occurring within the landscape (Blaszczynski 1997).

Topography and geology of watersheds have a major impact on the hydrological, geomorphological and biological processes operating within the landscape (Moore et al. 1991). Glacier Bay has experienced an extreme uplift since the Little Ice Age with the collapse of the Glacier Bay Icefield, which alone is equivalent to an 8mm rise of the global sea level (Larsen et al. 2005). Hydrology and climate will become impacted as well as being the main drivers for change in morphology over time. Day (1983) showed a dynamic balance between watershed rainfall and drainage, which was moderated by the attributes of the

watershed. Topology and geology are the two main factors controlling erosion, deposition as well as succession and vegetational development. Horton (1932) proposed five descriptive factors of a watersheds related to its hydrology; morphologic-, soil-, geologic-structural-, vegetational- and climatic-hydrologic factors. The key factor in the evolution of mountain landforms is channel initiation (Imaizumi et al. 2010), and the closer a channel starts to the drainage divide, the more finely dissected the watershed will be, as greater number of channels will occupy a unit area (Montgomery and Dietrich 1988). Automated channel initiation is therefore manly limited by the threshold of the contributing area (O'Callaghan and Mark 1984).

River channel morphology is dependent on the geology and climatic environment over long periods of time, but during shorter periods channel morphology is an independent variable influencing the hydraulics of the river channel (Schumm and Lichty 1965). Milner et al. (2011) suggested that macroinvertebrate community assemblage in newly emergent streams was strongly deterministic, while microcrustacean assemblies were more stochastic. Ziemer (1973) showed correlation between drainage system geometry and freshwater production of anadromous fish on a watershed scale, and (Swanston et al. 1977) used quantitative geomorphic variables to assess 78 watersheds in relation to pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*). To detect the different effects of disturbance on a given biological response variable, both the appropriate spatial and temporal scales are required (Poff and Ward 1990). These scales create a habitat that will provide the templet upon which characteristic species traits are forged by evolution (Townsend and Hildrew 1994). Organisms and habitats are part of a system linked with feedback (Southwood 1977), where life- and landscape dynamics are intertwined by feedbacks of different strengths and importance, and coevolution represent the tightest link between biological and geomorphological systems (Reinhardt et al. 2010). Factors operating at several spatial and temporal scales influence the state of the physical habitat (Medeiros et al. 2008), and the spatial heterogeneity is regarded as one of the most important factor in governing community

structure (Poff and Ward 1990, Stein et al. 2014, Yang et al. 2015). Phillips (2007) introduced the "perfect landscape" which would open up for multiple outcomes, as cause and effect in developing landforms is a function of time and space. Which could be either dependent or independent of variables as time and space change (Schumm and Lichty 1965). This hysteresis makes understanding landscape change within time and space difficult, including the testing of hypothesis (Montgomery and Dietrich 1992). Landforms are dependent on structure, processes and time (Davis 1899), and the scale of investigation determines the range of patterns and processes that can be detected (Wiens 1989).

2.1.4 Remote sensing

Remote sensing is recognized as a powerful method to map abiotic and biotic factors and to estimate their change over time (Rocchini et al. 2013). Several methods for acquiring surface topology have been developed, and accuracy has increased with better sensor technology. Smaller scales of measurement can more readily be analyzed with unmanned aerial systems (UAS) and handheld equipment. Integration of remote sensing into ecological research has great potential, since it remotely measures direct physical attributes at a point in time. Different softwares and algorithms have been developed to analyze digital elevation models (DEM's) and to facilitate incorporation of *in-situ* and field measurements, and these have played an increasingly important role in the field of biogeography over the last decade (Foody 2008). Digital representation of surface topology is useful to describe morphological features, and as deviation between elevation at one specified point and its true value diminishes, accuracy increases. Drainage networks are significant in modeling landscape development and drainage basin hydrology (Mark 1984), and DEMs are useful data sources from which drainage characteristics automatically can be derived (Jenson 1985, Tarboton and Ames 2001). Software tools which can derive morphological information from DEMs are useful in hydrological applications (Jenson and Domingue 1988). Melton (1958) pointed out that the

most obvious source of error would be the accuracy of maps, and therefore failure to show all channels and correct lengths. Field mapping is acknowledged as the most accurate way of analyzing drainage networks, despite its impracticality for inaccessible and vast areas (Tarboton and Ames 2001). Scaling is more a question of the quality of the remote sensing data, as this will determine the scale of what can be observed.

The aim of this paper is to present a framework for the PHT, and its development based on the morphological features within watersheds of different age since ice recession. Creating a PHT to use in a conceptual model will help to better understand the spatial and temporal changes in physical habitats and processes in watersheds which influence biotic communities. Integration of the PHT into a Minkowski space (Minkowski 1908) creates a four-dimensional point/resolution PHT layer system (x,y,z,t). Combining field and data to a continuum system will provide better understanding of the processes and patterns on a spatial-temporal scale. The conceptual model describes the development with time, and how space and time is related to scale and resolution. This can help explain the directional development in a four dimensional space, since the temporal component is stored in space-time geometry (Hazelton et al. 1990).

2.2 Methods

2.2.1 Study area

Watersheds are found in a chronosequence since LIA in Glacier Bay National Park. Glacier Bay has a strong tidal activity and a maritime climate, situated in the Pacific temperate rainforest region, with mild winters and cool summers. Glacier Bay consists of a complex fjord system with two major arms, West arm and East arm, approximately 59 km and 48 km. Study streams were located from the upper part of the east arm to the lower bay area. The studied watershed included Stonefly Creek (SFC), Wolf Point Creek (WPC), Ice Valley Stream (IVS), Berg Bay South Stream (BBS), and Rush Point Creek (RPC) and ranged in age from 39 to 207 years (Figure 2.3). Stream age was determined using satellite and aerial photos, historical data, journal articles and unpublished data as outlined in Milner et al. (2000).

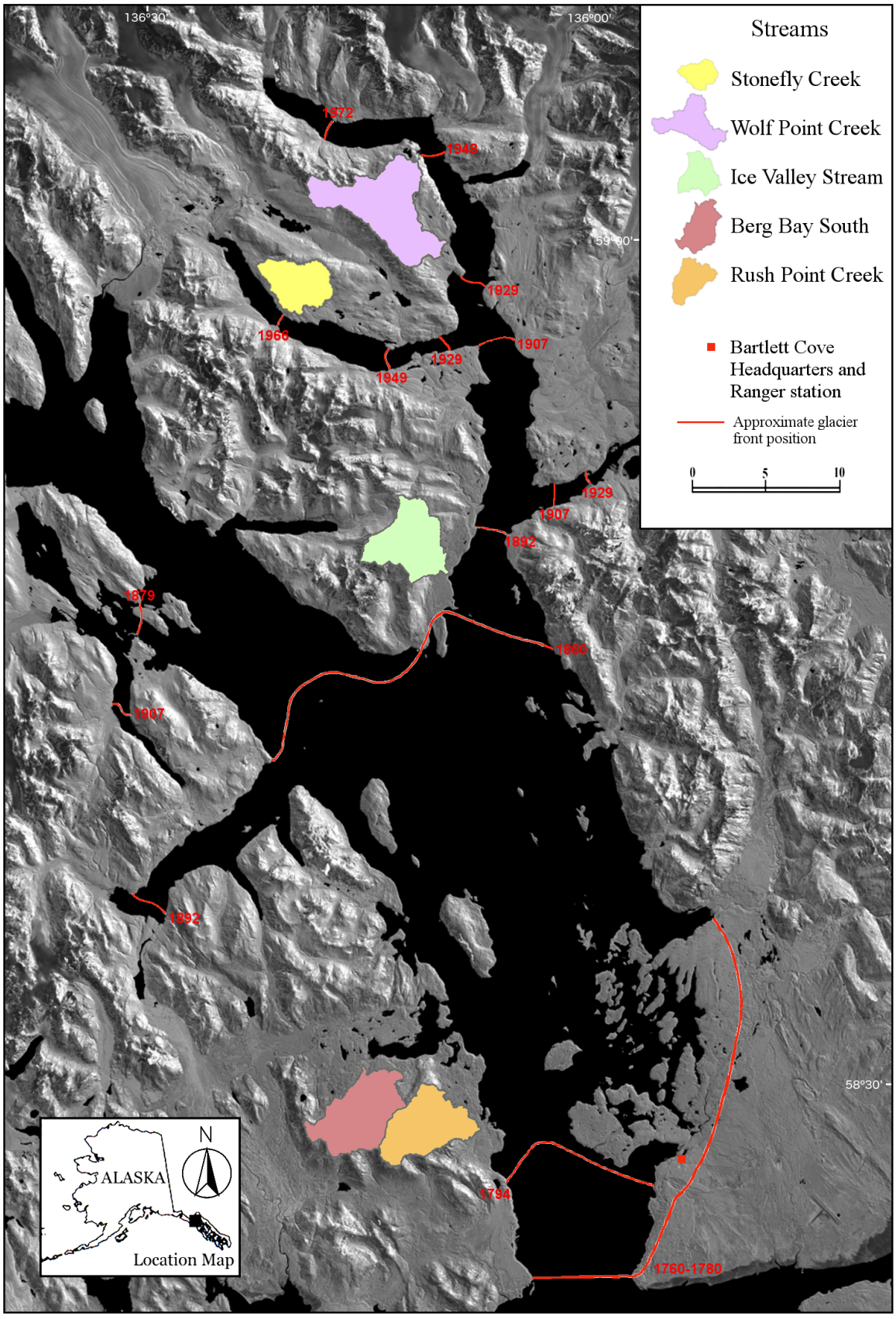

Figure 2.3: Study watersheds in Glacier Bay National Park, Alaska.

2.2.2 DTM mapping and data analysis

Digital elevation models were used to automatically map watersheds and stream network in Glacier Bay. IFSAR 15 x 15m tiles collected by Fugro were used to calculate morphological data. ERDAS IMAGINE v. 15.1 was used to mosaic the DEM tiles together, before areas with the watersheds of interest were cut out to limit the region size. Various variables are then calculated to produce valuable information regarding the watersheds geomorphological features. Watersheds were then extracted in GRASS 7 with the modules r.stream.basins and r.water.outlet, after using r.stream extract to find the stream mouth, and high tide from field observations were used as outlet points for the streams. This only varies for the streams BBS and RPC, which would get a larger watershed area with low tide, due to streams flowing together between low and high tide. Attribute Table Manager in GRASS 7 was used to calculate area, perimeter and compactness from the polygon created from the raster map (Table 2.1).

Stream delineation was undertaken with r.stream.extract, which uses multiple flow directions (MDF) which seem to give a more accurate stream network (Jasiewicz and Metz 2011). After first stream extraction from the DTM, errors found in the newly created stream network where changed based on field and aerial observations and patched in the DTM with d.rast.edit, before delineated again with r.stream.extract in GRASS 7. One percent of flow accumulation was used as a threshold as only most tributaries in SFC are known. This gives a strong underestimate of stream network, but will be the same for all watersheds, and make comparison possible. Stream network calculations were undertaken with r.stream.stats.

Elevation and slope (r.slope.aspect) data from the raster maps (DTMs) was calculated with r.univar, and contour line map was done with r.contour. While stream azimuth, sinuosity and basin (watershed) length was calculated with Attribute Table Manager after polyline was created based on main channel polyline from Hack in r.stream.stats.

Vegetation area was calculated from the watershed polygon, derived from digital surface model DSM minus DTM with r.mapcalc, and provide a good indication on vegetational coverage. Due to not having the x-band to correct for backscatter, there are smaller errors in the hight of the vegetation, and this is therefore not used as a parameter for vegetation succession. The total amount of lentic waterbodies (lakes, kettles and ponds) was calculated from polygons of known waterbodies, and therefore was likely underestimated.

Topographic wetness index (TWI), was calculated with r.topidx in GRASS GIS by $\ln(a/\tan\beta)$ where a is the upslope area draining through a certain point per unit contour length, and $\tan\beta$ the local topographic surface slope (Δ vertical /Δ horizontal).

Hypsometric curves (area-altitude curve) were created with the use of SAGA GIS v. 2.14. Due to the use of dimensionless parameters, curves can be described and compared irrespective of true scale (Strahler 1952).

2.2.3 Statistics

Spearman-Rank correlation was calculated for stream variables (Appendix 1) and principal component analysis (PCA) was used to assess directional relationship between the different watersheds using RcmdrPlugin.NMBU in R 3.1.2 (GUI 1.65).

2.3 Results

The study watersheds were different from each other according to location after deglaciation. While SFC sits on the margin of the U-shaped valley creating Watchusett inlet, with an upper clearwater lake (0.52km^2) and a lower lake (0.09km^2) still influenced by glacial runoff from remnant ice. WPC is created by a side glacier, next to the main fjord, with a paternoster lake system at the head of the watershed. One larger main lake (1.20km^2) and two smaller lakes above (0.13km^2 and 0.90km^2) feed the stream. IVS once was a glacier side arm, and have a main channel with an even slope up to the east side of the watershed. IVS was the watershed least influenced by lakes with only a few wetlands and smaller muskeg waterbodies. BBS is a watershed created from the retreat of a major glacial outflow which flowed east into the fjord. BBS has several glacial erosion cirque formations, and a cirque kettle lake (0.09km^2) at the upper end of the watershed. Like BBS, the RPC watershed was created after the retreat of a side glacier flowing eastwards into the fjord with a few glacial erosion cirque formations, and a hanging valley at the west end of the watershed. The RPC watershed supported smaller waterbodies due to several beaver dams and two small lakes. All streams have barriers in the mid-lower main channel except for IVS. Vegetation cover was different from watershed to watershed, with taller vegetation in older watersheds. (see Table 2.1 for a summary of watersheds characteristics).

Table 2.1: Characteristics of the study watersheds.

Variables	Watersheds					PCA	Reference	Formula
	1SFC	2WPC	3IVS	4BBS	5RPC	NR		
Age	39	65	141	181	206	N1	-	-
Area (km^2)	13,112	29,679	19,042	22,444	20,142	N2	Grass	Attribute Table Manager
Area elevation bellow 50m (km^2)	3,366	2,859	1,052	2,124	4,170	N3	Grass	r.mapcalc
Basin length (km) (Lb)	6,422	13,249	10,202	10,416	10,476	N4	Grass	Attribute Table Manager
Circulatory Ratio (Rc)	0,421	0,250	0,352	0,307	0,370	N5	Miller (1953)	$Rc = 4\pi A/P^2$
Compactness	1,540	2,000	1,684	1,806	1,645	N6	Grass	Attribute Table Manager
Constant of channel maintenance	0,604	0,854	0,702	0,654	0,622	N7	Schumm (1956)	C=1/Dd
Drainage density	1,656	1,171	1,424	1,528	1,609	N8	Grass	r.stream.stats
Elongation Ratio (Re)	0,636	0,464	0,483	0,513	0,483	N9	Schumm (1956)	Re=2*sqrt(A/pi)/Lb
First order streams length (km)	12,244	17,699	15,276	14,261	17,388	N10	Grass	r.stream.stats
Fitness Ratio (Rf)	1,095	0,896	1,034	1,125	1,238	N11	Melton (1957)	Rf=Lu/P
Form Factor Ratio (F)	0,318	0,169	0,183	0,207	0,184	N12	Horton (1932)	($F=M/L^2$) $Rf=A/Lb^2$
Hack mean main channel elevation diff. (m)	501,120	585,240	507,950	389,840	376,710	N13	Grass	r.stream.stats
Hack mean main channel gradient	0,082	0,049	0,054	0,041	0,039	N14	Grass	r.stream.stats
Hack mean main channel slope	0,086	0,055	0,061	0,062	0,058	N15	Grass	r.stream.stats
Hack main channel (km)	6,138	11,843	9,474	9,552	9,727	N16	Grass	r.stream.stats
Length Area Relation	6,557	10,705	8,203	9,053	8,484	N17	Hack (1957)	Lar=1.4*A^0.6
Length of overland flow (Lo)	0,303	0,429	0,353	0,329	0,311	N18	Horton (1945)	Lg=A/2*Lu (Lo=1/2Dd)
Length ratio (Ll)	2,6598	3,2003	3,1825	3,6152	2,5972	N19	Grass	r.stream.stats
Main channel azimuth	203,812	95,183	85,926	21,024	58,187	N20	Grass	Attribute Table Manager
Main channel sinuosity	1,672	1,342	1,743	1,685	1,556	N21	Grass	Attribute Table Manager
Max watershed slope in degrees	63,901	73,633	74,242	69,853	69,060	N22	Grass	r.univar
Mean Bifurcation ratio (Rb)	4,800	5,375	3,167	3,167	3,587	N23	Grass	r.stream.stats
Mean watershed elevation (m)	214,078	357,247	314,275	228,816	232,796	N24	Grass	r.univar
Mean watershed slope in degrees	16,091	21,777	20,836	18,075	17,449	N25	Grass	r.univar
Median watershed elevation	94,180	291,710	271,470	203,580	188,860	N26	Grass	r.univar
Median watershed slope degrees	13,630	20,677	20,808	16,441	15,105	N27	Grass	r.univar
Melton ruggedness number	0,195	0,227	0,217	0,156	0,173	N28	Melton (1965)	(Zmax-Zmin) / A(squared)
Perimeter (km)	19,788	38,628	26,056	30,326	26,168	N29	Grass	Attribute Table Manager
Relief (m)	705,910	1235,130	947,960	738,270	774,450	N30	Grass	r.univar
Relief Ratio (Rhl)	110,457	93,525	93,184	71,293	73,927	N31	Schumm (1956)	Rhl=H/Lb
Rho	0,554	0,595	1,005	1,142	0,724	N32	Horton (1945)	$\rho = r_l / r_b$
Stream. Freq. (n)	2,216	1,083	2,008	1,702	2,433	N33	Grass	r.stream.stats
Stream order	3	3	4	4	4	N34	Grass	r.stream.stats
Total number of streams (Nu)	29	32	38	38	49	N35	Grass	r.stream.stats
Total stream length (km)	21,670	34,608	26,940	34,115	32,398	N36	Grass	r.stream.stats
Waterbodies (km^2)	0,739	1,482	0,005	0,098	0,026	N37	Grass	r.mapcalc
% Vegetation in the watershed	72,431	50,620	70,232	71,970	77,214	N38	Grass	r.mapcalc
% Waterbodies in the watershed	5,632	4,993	0,024	0,436	0,131	N39	Grass	r.mapcalc

The two youngest watersheds had stream order 3, while the rest had stream order 4 (Figure 2.4). Vegetation cover (Figure 2.5) and areas with lower slope in degrees match up (Figure 2.6). All five streams had a mean bifurcation ratio > 3, with WPC exceeding 5. Drainage density was found to be lowest in WPS and IVS (< 1.5), which are the watersheds with highest relief and ruggedness. Highest drainage density was found in SFC and RPC, which were the watersheds with large areas < 50m, containing large parts of the main channel. WPC and IVS have areas within the watershed with the lowest and the highest TWI (Figure 2-7), mean watershed slope and the lowest drainage density among the watersheds, while SFC and

RPC had the highest low TWI values, the lowest mean slope and the highest drainage densities. BBS showed the highest Rho while SFC and WPC had the lowest Rho. Vegetation and total number of streams correlated positively with watershed age, while relief ratio correlated strongly negatively with watershed age. Percentage of vegetational cover also correlates with elevation < 50m, and correlates highly positivity with drainage density, stream frequency and fitness ratio. Percentage of vegetational cover correlates negatively with all factors relating to elevation, except for mean main channel slope. Water bodies correlated strongly negatively with watershed age and length of the basin and are seen with 25m contour lines in Figure 2.8.

Main channel longitudinal profiles for each stream show the elevation (m) at the start of the main channel and the length of the main channel (m) (Figure 2.9). Elevation at the start of the main channel of WPC was highest at 584m while RPC was the lowest, starting at 385m. The length of the main channel of WPC was longest with 10871m, and RPC the shortest with 8810m. Main channel longitudinal profiles also show larger barriers along the main channel. Large differences in the relief ratio between the different streams, where the youngest stream had the highest and the two oldest having the lowest relief ratio values (Table 2.1). The hypsometric curve is similar for all streams except for SFC (Figure 2.10). Correlations of the features among the watersheds are found in Appendix 1. The PCA in Figure 2.11. shows the position of the watersheds in relation to each other, and show that BBC and RPC is the most similar watersheds, while SFC and WPC are positioned furthest from each other in PCA space. The percent vegetation cover positive relationship with watershed age and the relief ratios negative relation to watersheds age indicate vegetational succession and that the relief ratio decreases over time since deglaciation and indicates erosion and denaturation over time. The “initial” stage affect the state of which the progression is in, while the pattern of denudation on the watershed and the stream channel by the temporal scale in Glacier Bay.

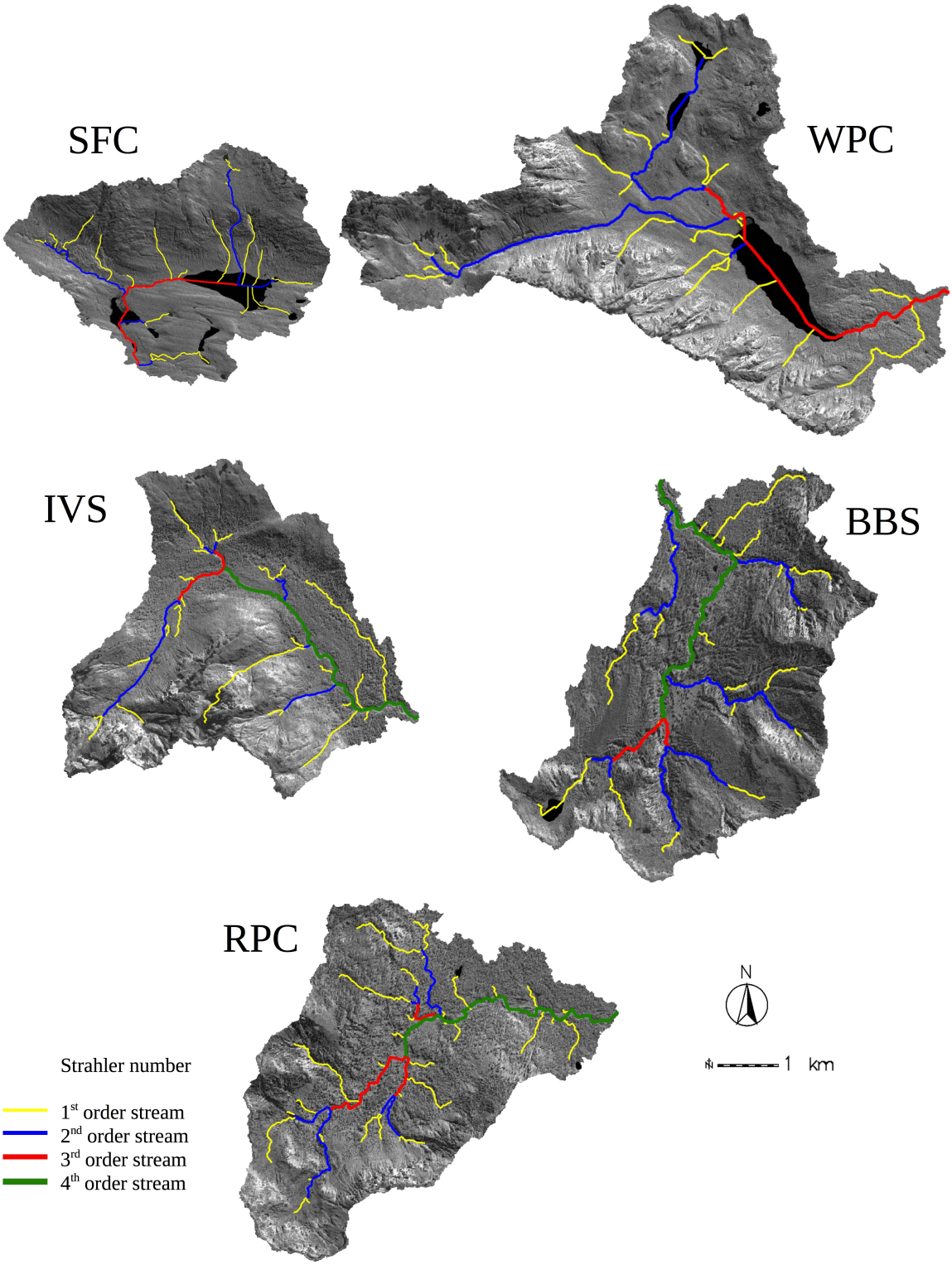

Figure 2.4: Watershed with stream order.

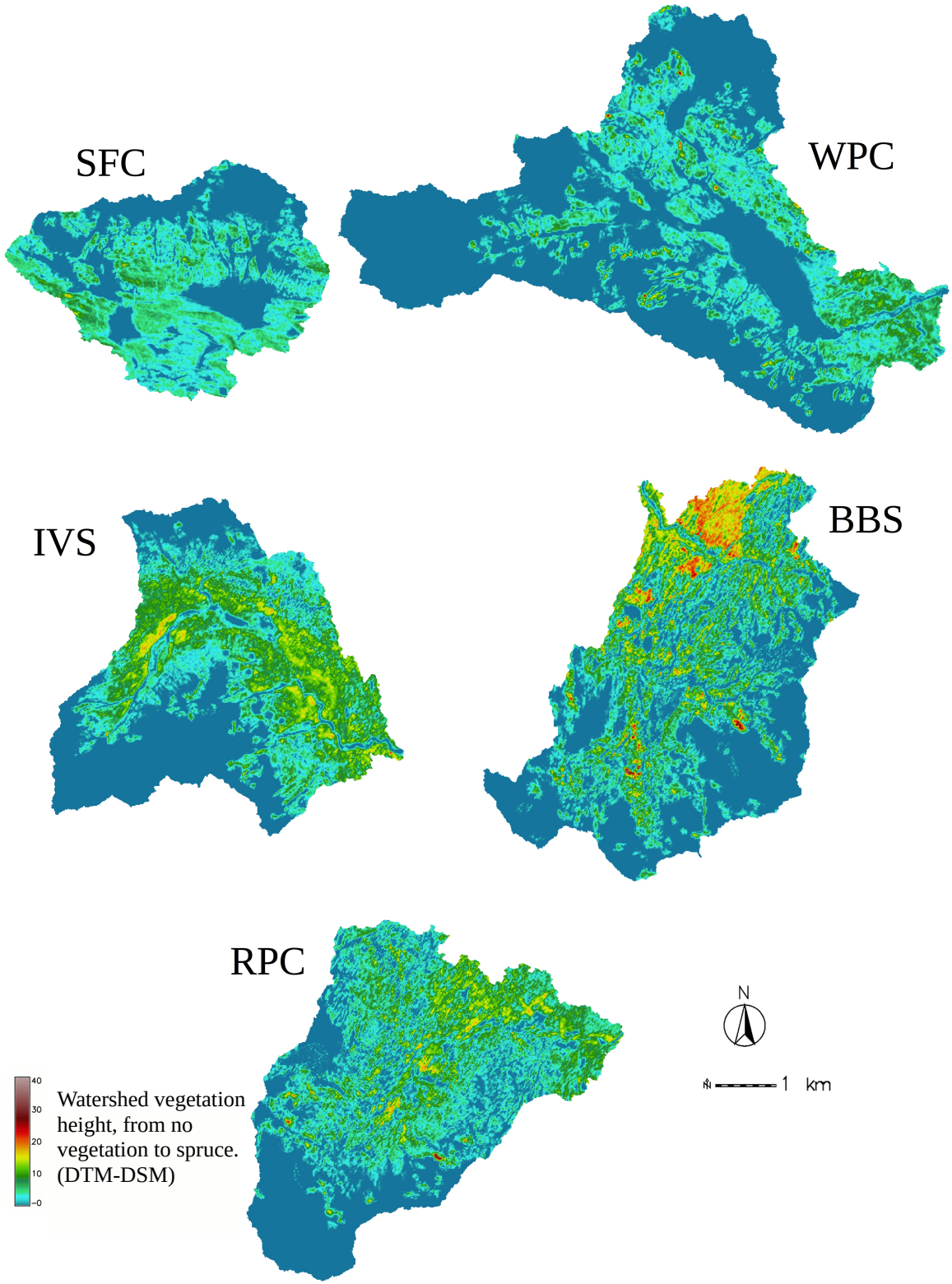

Figure 2.5: Vegetation cover and height.

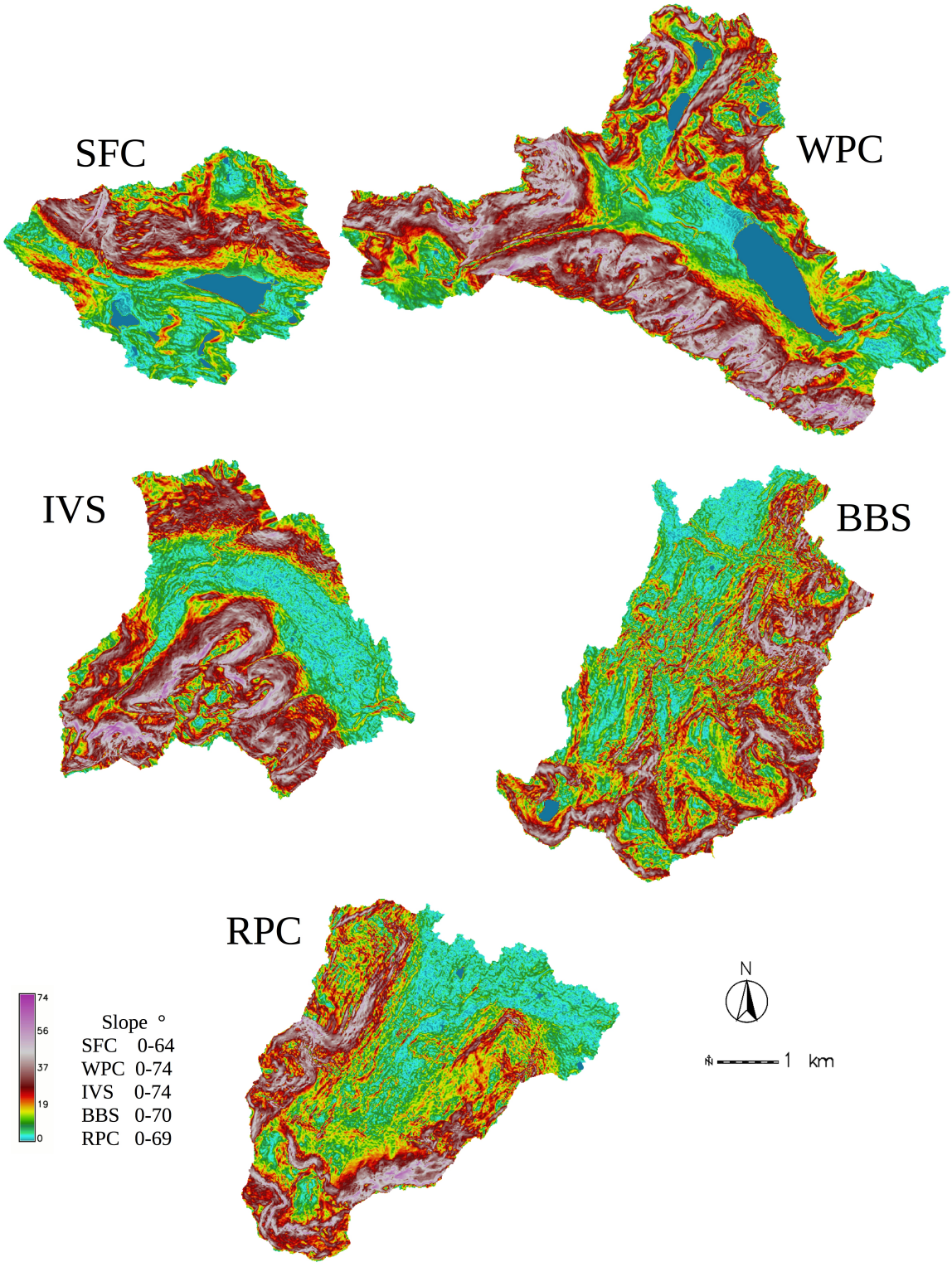

Figure 2.6: Watershed slope.

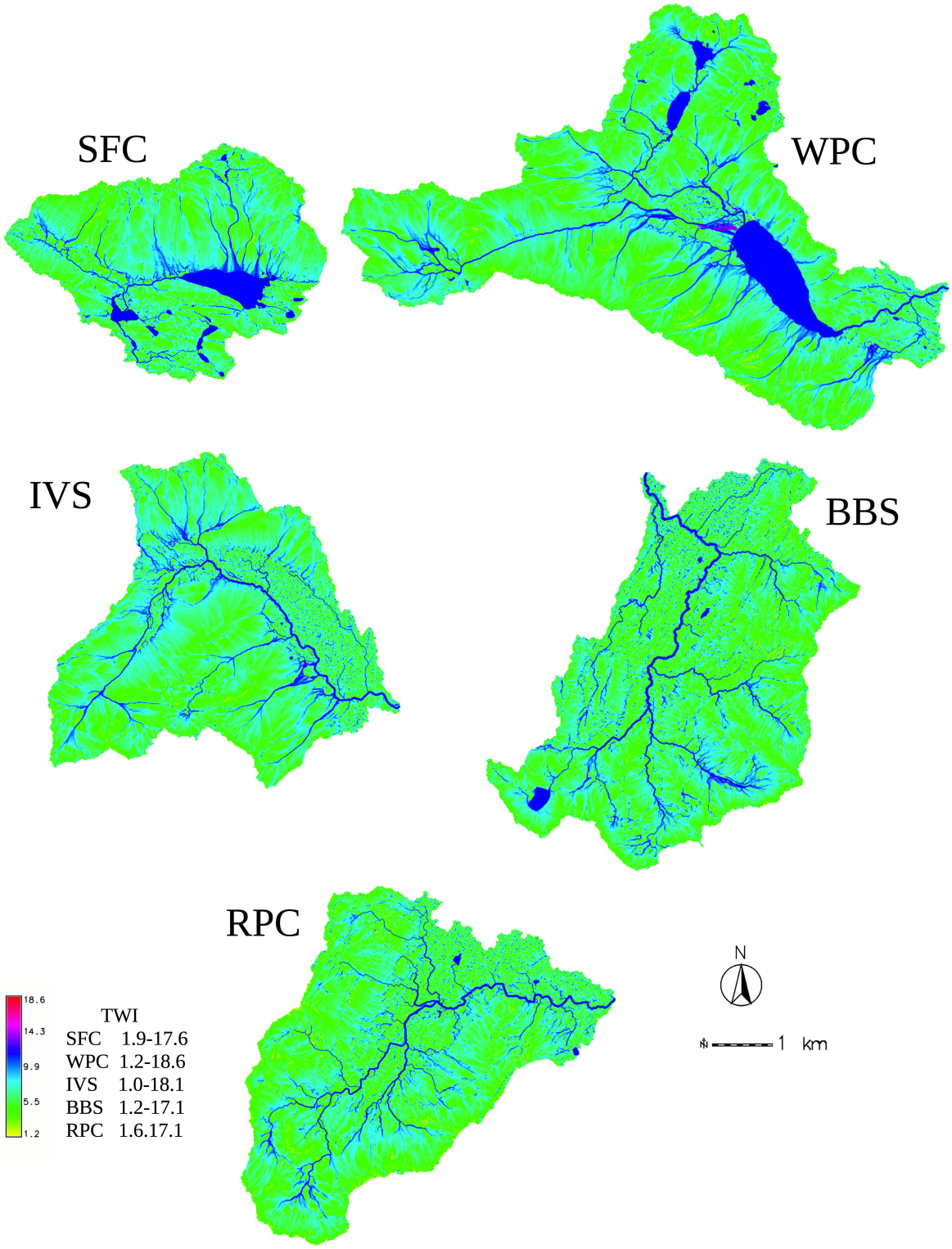

Figure 2.7: Watershed topographic wetness index (TWI).

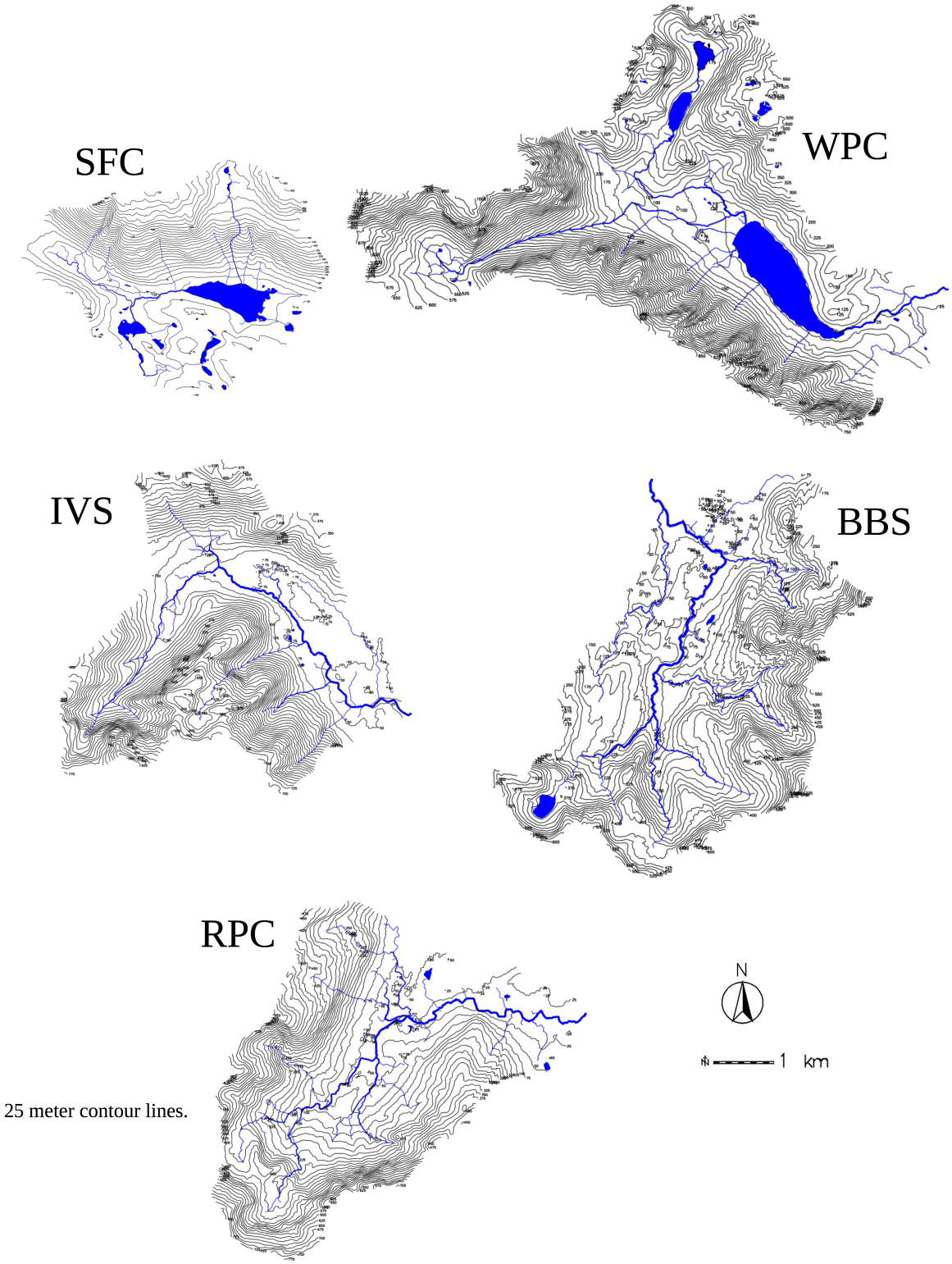

Figure 2.8: Watersheds with 25 meter contour lines, lakes, ponds, waterbodies and stream system.

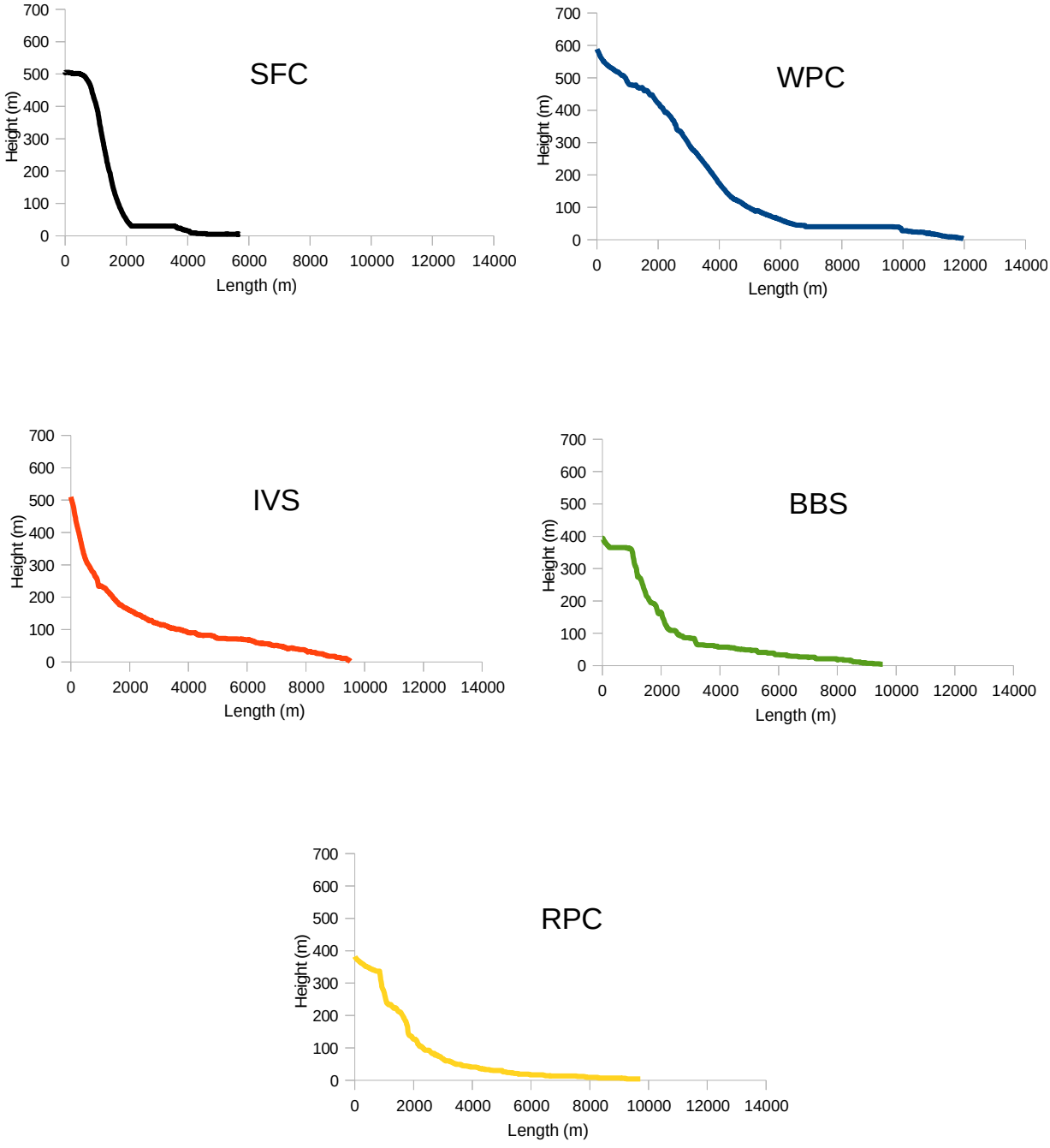

Figure 2.9: Main stream channel profile.

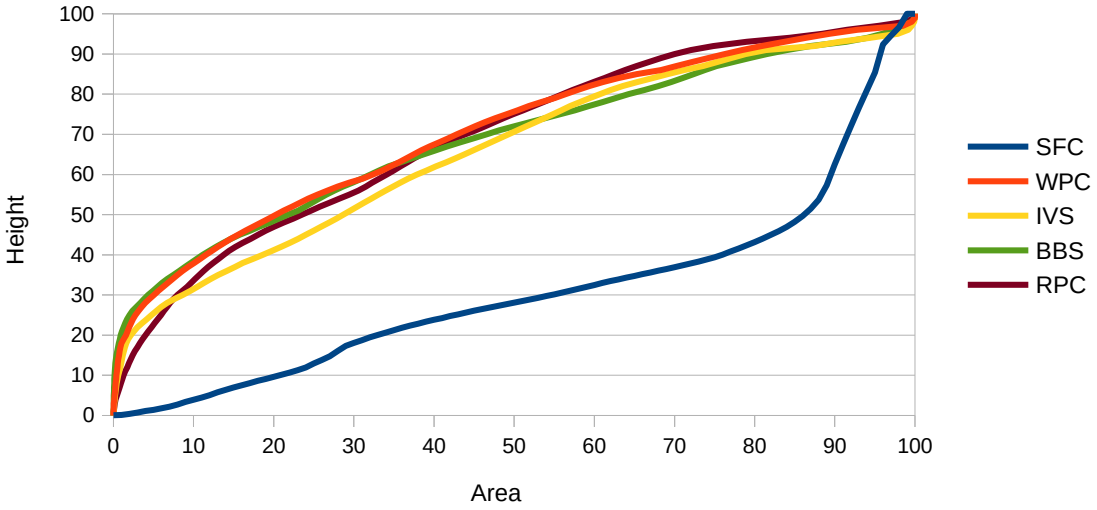

Figure 2.10: Watersheds hypsometric curve.

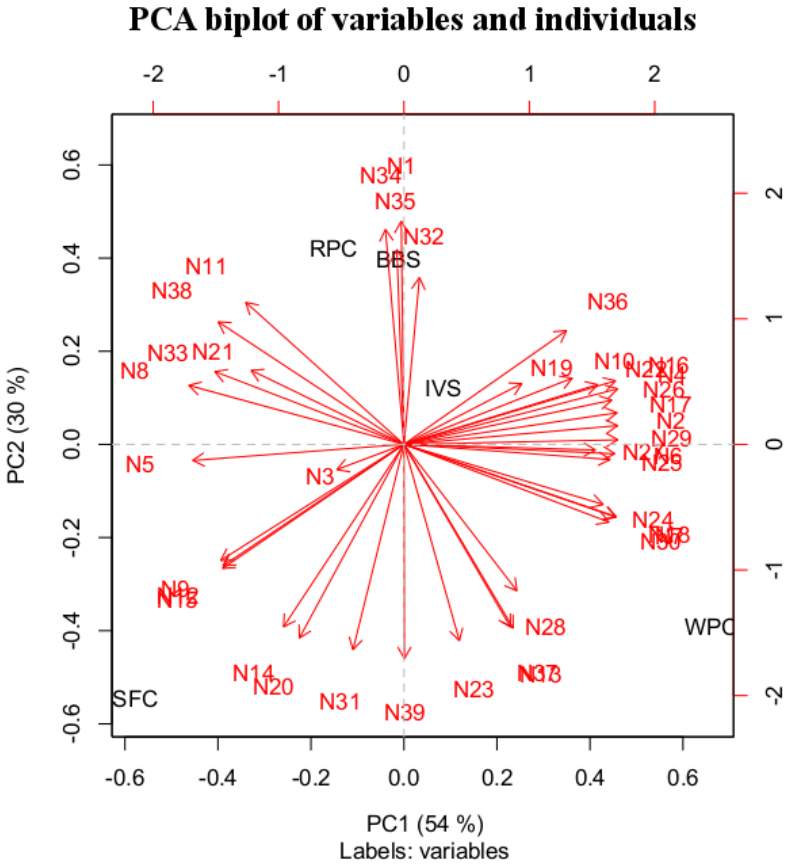

Figure 2.11: PCA of all the watershed variables.

2.4 Discussion

2.4.1 Scale and resolution

Remote sensing can be used in relation to most scales, but to cover larger spatial scales, like a watershed, use of satellites and aircraft remote sensing are the more reasonable method, as handheld remote sensing is time consuming. Resolution of the point cloud/volume at a certain scale will determine what processes and patterns that can be detected. The use of UAS will increase the spatial scale and is a good alternative in smaller scale investigations. Fusion of different remote sensing at the same resolution and scale will increase the knowledge of interconnection of landscape systems and biomes. The increase in technological advances in remote sensing provide an improved resolution over larger scales and will contribute to a better understanding of watershed development and the effect on the biology and the populations within, for instance salmonids. The current accuracy of remote sensing shows a vast improvement from Klaar et al. (2015). This study used watershed delineation from 1997 (Geiselman et al. 1997), which cut upper SFC lake in half, creating the impression of a lake draining in two directions. At WPC, an adjacent watershed is included in the WPC watershed. This will have caused a large error in the calculations of vegetation in the area, as well as the timeframe when the area was ice free. Improvement from earlier watershed delineations differ > 10 km^2 in watershed sizes and > 400 m in elevation from Klaar et al. (2015), causing vast difference in vegetation estimates. The accuracy is therefore very important, combined with field/aerial observation to make sure that the delineation is correct. Increased accuracy will therefore better describe the physical habitat and provide a more realistic template to assess ecological processes and patterns including the temporal effect. New remote sensing technologies in years to come will provide much higher resolution then these IFSAR data used in this paper.

2.4.2 Ecogeomorphology

Post-glacial colonization by freshwater organisms in these newly emerged watersheds (Milner and Bailey 1989) seem to be controlled by geomorphological features. Results here show topology to be the controlling factor in both vegetation and stream development. The temporal effect seem to vary depending on the watershed geomorphology, where development occurs at a faster rate at lower elevations. WPC and IVS are slightly more rugged than the rest, and all watersheds are third to fourth order streams, where very rugged areas rarely exceeds 1.0 (Melton 1965). Longitudinal profiles of the main channel provide a good indication of the main channel source elevation, the length of the main channel and larger change in slope, like possible barriers for fish and the presence of lakes, which can be observed from the profiles (Figure 2.7). The even slope up to the east side of IVS watershed, create no barriers for juvenile or spawning salmonids. The youngest stream SFC has a small barrier downstream from the upper lake, which can be hindering salmon migration. Despite this juvenile Dolly Varden (*Salvelinus malma*) has been trapped above this barrier. WPC has a large barrier which most likely will hinder all salmonid migration. BBS and RPC also have a barrier longer up the main channel. With the use of UAS or handheld remote sensing equipment smaller differences can be observed and all barriers for fish migration assessed. The longitudinal profile only shows lakes that are directly in line with the main channel, and the upper lakes in WPC does not connect when using Hack, since the longest channel stretches up the north-west side of the watershed. The profile also shows the length of the main channel and the height above sea level, where WPC starts at a higher elevation and is several thousand meters longer than the other streams. The lowest start elevations are found in the two oldest streams. High bifurcation ratio indicates mountainous or highly dissected drainage basins (Horton 1945), and bifurcation ratio are one of the factors controlling the rate of discharge (McCullagh 1978). Erosion, denudation and strong glacial isostasy form the landscape and are strongly important for succession and watershed morphology changes. Watershed topology influences the operation of the hydrologic cycle, runoff in particular (Horton 1932). The higher bifurcation

ratio in WPC and SFC indicates a likelihood of a shorter lag time and higher peak discharge. Main stream longitudinal profiles were similar to the drainage basin profile (Horton 1932), which would furnish the best basis for comparison of elevation with hydraulic characteristics of the drainage basin. Mean watershed slope can be related to denudation of the watershed. The low value for SFC is due to the location of the watershed, most of which is located in the lower margin of the U-valley creating the fjord of Wachusett Inlet. The relief ratio (Rhl) is the total difference from top to bottom of the watershed and seem to be a better measure for estimating the denudation effect with time, even though the timeframe in Glacier Bay is only a few hundred years. Dividing the landscape into watersheds can therefore also be a good way to understand the change in the overall landscape. Drainage network extraction depends primarily on the accuracy of the maps used and the identification of the channel initiation (Lin et al. 2006). The only stream with known tributaries was SFC, and by georeferencing the map created in arc-map in 2004 a more accurate threshold would be around half of 1%. This will vary from stream to stream, and thus 1% flow accumulation was used. Smaller tributaries are therefore not present on the stream maps, as the initiation threshold is the same for all streams. Stream channel erosion, associated processes of weathering and sheet runoff creating topography is extremely complex (Strahler 1952), and a mixed vegetation would almost certainly provide the best bank stability, and potentially benefit the riparian habitat the most (Simon and Collison 2002).

Drainage density is an excellent indicator of permeability of the surface of the drainage basin (Horton 1932). This texture of dissection of the watershed will be an underestimate due to the 1% of accumulation threshold. The drainage density values are therefore lower than what it should be, but the underestimate will be equal for all streams. Drainage density was found to be lowest in WPS and IVS, suggesting higher infiltration and less direct surface runoff. WPS and IVS are watersheds with higher relief and ruggedness and large amounts of observed sediments, as these watersheds are similar in glacial sediment depositions. TWI is commonly used to quantify the control of topology on hydrological processes (Sørensen et al. 2006).

Moore et al. (1993) found slope and wetness index to be the terrain attributes that correlated the most with surface soil attributes. Area topology controls the TWI, and highest mean watershed slope and the lowest drainage density was found in WPC and IVS, which has the lowest and the highest TWI. While SFC and RPC are the watersheds with the lowest mean slope and the highest drainage densities and has the highest low TWI values. This shows that WPC and IVS have variated terrain, with crests, ridges and drainage depressions.

The ordering of streams was done using the method of (Strahler 1952) and is an underestimate of the rest of the stream networks due to the 1% threshold. The higher Rho values the greater the length of larger stream channels to potentially increase channel storage per unit of drainage area. This increase can sustain channel flow for longer periods of time after channel inflow from surface runoff (Horton 1945). BBS had the highest Rho and would potentially increase the storage compared to other streams, while SFC and WPC had the lowest Rho and storage, which would potentially drain out quicker. Stream numbers increase with age in Glacier Bay due to the creation of top soil and vegetation, causing less permeability and in turn higher number of streams to drain the watershed. Cotton (1964) found that drainage densities (texture dissection) are coarser on permeable compared to impermeable terrains, and that this was an easily observed fact. IVS has the lowest Dd (drainage density) with variable flow and highly permeable stream bed, as water was absent from the stream bed close to the mouth on several occasions.

The distribution of ground surface area can be studied through hypsometric analysis (Strahler 1952), an empirical cumulative distribution function of elevations in a watershed creating an hypsometric curve. A dimensionless parameter comparable among watersheds, without taking into account the true scale (Strahler 1952). Readily available as a continuous parameter, the curve form can be troublesome to quantify (Harlin 1978) as relief ratio and stream gradient obtain a constant value when approximately 25% of the mass of the watershed has been eroded and watershed shape becomes constant after 40% mass removal (Schumm 1956).

Strahler (1952) introduces an inequilibrium stage, an equilibrium stage and a monadnock phase, relating to young, mature and old stages. The youngest stream in this study occur in Figure 2.10 as a mature, older watershed according to Strahler. The hypsometric curve here is clearly controlled by the shape of the landscape. Vivoni et al. (2008), showed that the hypsometric curve exerts control on surface and subsurface runoff, where relatively less eroded (convex) watersheds display a higher total runoff, which is dominated by subsurface processes, while more eroded (concave) watersheds show less total runoff with higher surface response. The form of the hypsometric curve (Strahler 1952) reveals clear signatures on the spatial distribution of soil moisture and runoff response mechanisms (Vivoni et al. 2008).

2.4.3 PHT of a riverscape

The PHT provided here is based on measurements analyzed from IFSAR remote sensing data, but there is virtually no limit on adding layers of water temperature, discharge, geology or remotely sensed wind measurements within the watershed etc. Remote sensing can be used at different scales, for instance describing microhabitats. However, by reducing the scale the overall picture and the patterns and processes affecting the micro habitat can not be observed. There are almost an infinite number of elements affecting the PHT, and temporal influences come and go depending on the spatial and temporal scale, but the more layers of parameters at point t, the more complete PHT that can be created. Rather than simplifying the complex environments present, the idea here is to combine the collected or analyzed data available into a PHT. This way larger or smaller scales would more readily be analyzed alone, together, and combined for further work. All levels within the river watershed potentially provide mechanisms to maintain biotic diversity (Medeiros et al. 2008), and the PHT can therefore help to understand difference in community both in and among streams. If developed into a common platform, the PHT can be used as a base in any discipline. Data from different biomes across the world can be compared, due to the common platform of PHT scale. Having a common platform, datasets can be compared, and temporal aspects and climatic changes

analyzed. Remote sensing can include wind speeds, temperatures and rainfall, and when fused into a three-dimensional PHT, this will create a strong basis for an understanding of the watershed. The more layers that are combined in a continuum, the more temporal information can be extracted, like fluxes of temperatures, stream discharge, biomass growth, or salmonid population migration within the watershed throughout the summer. The PHT concept will be the same for any scale and resolution.

2.4.4 Directional development of the PHT

Vegetation cover is different from watershed to watershed, but successional growth appear to follow the age of the watersheds. The position in PCA space is a strong indicator that the initial state after deglaciation is the controlling factor for which direction the watershed will take in regard to colonization and succession, with vegetation cover as a proxy. Watershed age indicated an increased development of larger vegetation, and that this temporal scale has a clear relation to the position of the streams in a PCA plot space. Percent vegetation cover show a relationship with elevation < 50m, drainage density, stream frequency and fitness ratio, and the negative relationship with percentage vegetational cover with all factors relating to elevation, except for mean main channel slope. These relationships influence the percentage of vegetation cover and are stronger indicators of vegetation than stream age. Rossi et al. (2014) found the physical environment to be the controlling factor for vegetation patterns in mountain areas.

Vegetation may also exert significant control over fluvial processes and morphology (Hickin 1984), and in turn provide positive feedback to stream succession. Confounding factors like spatial and temporal scale, location, convergence, divergence, nonlinearity, thresholds, feedbacks making cause and effect linkages difficult between vegetation and hillslope (Marston 2010). Soil erosion rates are significantly controlled by vegetation, and water

erosion decreases exponentially with increasing vegetation cover (Gyssels et al. 2005). Watershed denudation over time change since deglaciation due to colonization and succession indicate that vegetation increases with time, and the growth of vegetation which is subject to the temporal aspect. Pollen (2007) found that bank stability was reinforced by vegetation during a range of soil moisture conditions, while the degree of root reinforcement varied both in space and time determined by soil shear strength and soil moisture. The location was observed to have a major impact on the succession and vegetation and is a strong deterministic factor, more so than time, in controlling succession. Feedbacks between geomorphology and vegetation is incomplete, and there is a complexity of multiple outcomes, with place dependent results (Marston 2010). A variety of factors influence the landscape change with time, and the reduction method to establish models might compromise the understanding of the pattern and processes. Due to the inherent coupling of biological and physical processes a clear timescale between vegetation and geomorphology on hillslopes might not exist (Marston 2010). A more concise method for determining change in a chronosequence may be evaluating the areas with a PHT, in order to understand more random changes.

Low water temperature and channel stability in glacier fed rivers can create a habitat template that selects for certain traits, suggesting deterministic processes (Milner et al. 2001, 2011). Deterministic controls exerted on colonization and succession are here suggested to be the controlling factor in watershed development, since initial landscape location and topology control spatial and temporal effect of colonization and succession of vegetation. While the processes for colonization and changes in succession can be random (stochastic) noise, the controlling factors for colonization and succession still remain deterministic. A random event of seed transport would still be controlled by wind patterns and fluctuations, as well as the end location and its morphology for success. Random events may essentially be controlled by a complexity of deterministic events. The vegetative effect of succession and a temperature

change would initially be a deterministic change due to change in the initial factors. Milner and Robertson (2010) suggested that stochastic mechanisms begin when water temperature exceeds 7°C. While possible random events will influence the course of colonization and succession, initial conditions have now changed and will result in a different trajectory. This paper suggests that deterministic chaos with the impact of noise as stochastic events control colonization and succession universally from small to larger landscapes.

Interplay of physical and biological factors develop natural ecosystems (Swanson 1980). The results from the correlation and PCA, show that the basic factors; slope, stream network and vegetation, are linked to the initial state of the watershed after deglaciation, and that the temporal effect is different depending on the initial state. Time since deglaciation significantly affects stream network and denudation of the watershed. Vegetation cover was significantly negatively correlated with mean watershed slope and length of overland flow, indicating less vegetation due to topography, and less overland flow where vegetation is present. The more layers collated into a PHT on the earth's surface at a point in time enhance the knowledge of interactions and processes within a watershed or spatial scale investigated. The whole watershed as a basis for a PHT, provide knowledge of patterns and processes in the watersheds and in river systems. Throughout the riverscape distribution patterns of salmon can be expected to change over time as a response to environmental conditions and population sizes (Flitcroft et al. 2014). When years of physical habitat data are collected, the temporal aspect, as a result of the PHT can be assessed, and knowledge about species attributes and traits, and life history strategies revealed. The interconnectedness of the watershed can more readily be observed and analyzed with increased resolution on a larger scale. The height, area of vegetation or biomass for each species can be possible to address with remote sensing. Cost and processing time will be the two major factors that control the choice of the investigator. With the development of better remote sensing equipment, analyzes of the ecological development will be improved.

The dynamics of pristine lotic ecosystems can be understood by applying a broad spatiotemporal perspective (Ward 1989). Due to the relative short age difference between watersheds and minimum anthropogenic influence, Glacier Bay is a perfect natural laboratory to understand processes in watershed and stream development. Figure 2.12 describes the direction of watershed development based on initial coordinates and stochastic impacts in a four dimensional space, giving the physical habitat present at point/resolution in time, 4D (PHT,t). The spatial textures within the watershed are the result of processes within, up to time t. The physical habitats are a result of a combination of all these factors. The processes and patterns behind the physical habitat can therefore give an insight into how they are formed. Deterministic chaos can be expected to have incidents of stochastic events, changing the direction of the deterministic chaos. The physical habitat template can continuously change due to impacts of noise, here as random stochastic events. The resolution will determine the rate of change than can be observed, as this will vary on a spatial scale and on the initial state of the PHT. The processes leading (history) to the present physical habitat are influenced by factors on spatial and temporal scales. The conceptual model presented shows that the physical habitat template can aid understanding of the watershed and stream development over time, and possibly understand the rate of chaos and stochastic events that drive change over time. The model gives a simple stepwise introduction to chaos and stochastic events in the development of the PHT. The (PHT,t_1) gives a snapshot of the watersheds PHT at time t_1. The three-dimensional integral between (PHT,t_1) and (PHT,t_2) are the actual change in a PHT temporally from point t_1 to point t_2, which provide the rate of the changes between (PHT,t_1) and (PHT,t_2). The conceptual model (Figure 2.11) describes how deterministic chaos and stochastic events control the direction of development. Where D_{TOTAL} is the direction of development from start to end of the observed/remotely sensed PHT at time t_5.

$\sum_{i=1}^{N_1} D_i$ = Sum of total directional development

C_i = Chaos

$\sum_{j=1}^{N_2} S_{1,j}$ = Sum of stochastic events

$D_{TOTAL} = \sum_{i=1}^{N_1} D_i = \sum_{i=1}^{N_1} \left(C_i + \sum_{j=1}^{N_2} S_{i,j} \right)$ = Total direction of development

The space in a four-dimensional system from point to point represents the change between them. Knowing what changes and the rate of change is highly useful in understanding the processes responsible for these transitions. Habitat suitability index models (Fish and Wildlife Service 1981), are often used to predict habitat quality and distribution of species (Zajac et al. 2015). When creating a conceptual model, the idea is to create a universal base for a PHT, which can be built on depending on location and biome of the PHT. There will always be a close to infinity range of parameters to analyze, but the basic geomorphology is the base and the controlling factor in watershed development, and are the same for hydrology, ecology etc. The continuous change and initial effect are important to keep in mind, as a change from natural habitats to restored habitats can change the biological communities in ways that are not intended. The conceptual model shows how remote sensing and GIS can be used to assess the rate of change in addition to the amount of change. By using a four-dimensional space, the change from point to point can be measured, and resolution and scale will be the limitations of what can or cannot be observed. The larger scale provides the opportunity to understand processes and patterns in watershed development. The use of a standardized three-dimensional physical habitat template created from analyzing remote sensing data will contribute to a better understanding of colonization, succession and chronosequences. The

pathway taken through time, affected by chaos and stochastic events can by continuously creating a physical habitat template for a watershed, aid in giving us an understanding of how to more accurately predict changes through time.

Analyzing the five watersheds in this chronosequence with GRASS GIS indicate that the change over time is strongly influenced by the initial geomorphology. Temporal pathways are affected by both chaos and stochastic events, which seem to start based on the trajectory from an "initial state", the present physical habitat template for the different watersheds. Multiple pathways of compositional change in Glacier Bay appear to be a function of landscape context in conjunction with species life history traits, which again alter the arrival sequence of species (Fastie 1995). The watersheds were observed to be altered by the initial topography, resulting in faster succession. This is without taking into account the spatial scale of dispersal and where from the colonizers might have come. Mapping ecosystems into discrete non-overlapping classes can cause uncertainties (Rocchini et al. 2013), as the spatial scales, temporal scales and processes will vary and influence each other, and not always be within ecosystems in a set time and space. No two places share identical histories, climate or topography and having randomly fluctuating environmental factors (May 1974). GIS can also be used to study landscape connectivity (Marston 2010), where stream channels are essential in linking watersheds and larger landscapes together. With new technology, a better understanding of physical processes at a larger spatial scale are possible. Nutrient cycling and retention and loss over time can also more accurately be estimated. GIS can provide information in assessing watersheds and their fish production for management and research purposes. This study illustrates that colonization of new stream systems can be extremely rapid, where a diversity of habitats is created following ice recession due to the difference in geomorphology. It does not seem to be one single direction of causality between life and its landscape; both simultaneously exert influence over each other over a range of spatial and temporal scales (Reinhardt et al. 2010). Deterministic chaos can help explain the unseen

connection between life and landscape. Extreme rapid colonization of new systems like in SFC (Milner et al. 2011) are a result of location and topography.

Pathways are, with the use of GIS over time more easily detectable, and the five watersheds analyzed indicated that initial factors are more important than the temporal effect. The use of chronosequences in studies are easily misused, particularly in relation to successional pathways of vegetation (Johnson and Miyanishi 2008). Due to the different initial conditions, the watersheds will not display a direct linear development with time. Initial conditions are therefore important when considering chronosequence studies of landscape morphology, evolution and vegetation. The more information that can be collected from the whole watershed, the more of the processes and patterns of the watershed and the inhabiting biota can be analyzed and assessed. Due to only five study streams and large differences in initial starting points after glacial retreat makes the significance of each correlation less reliable. The use of GIS to better understand the physical habitat is very helpful in managing biotic communities in the area. Continuous measurements of the PHT will create an unprecedented resource of data to better understand changes with time.

The shorter-term chronosequence in Glacier Bay provides a base for assessing possible change in succession based on the initial set of morphological factors present after glacial retreat. This seems to be the strongest factor in deciding for or against colonization and succession, and influence the timeframes of both. These are only five watersheds, and are not enough to develop a model which can predict ecological patterns and processes. These streams are used to show how the concept of a three-dimensional PHT could provide great knowledge on process and patterns with time, and give an understanding to how chaos can be predicted with the use of observed stochastic events, and the initial conditions from where development succeeds. Thus also understand processes among and in-between watersheds, and what processes are effectively outside impact and what is local from within the

watershed. Space-for-time substitution will be more predictable if it is based on the initial state geomorphology.

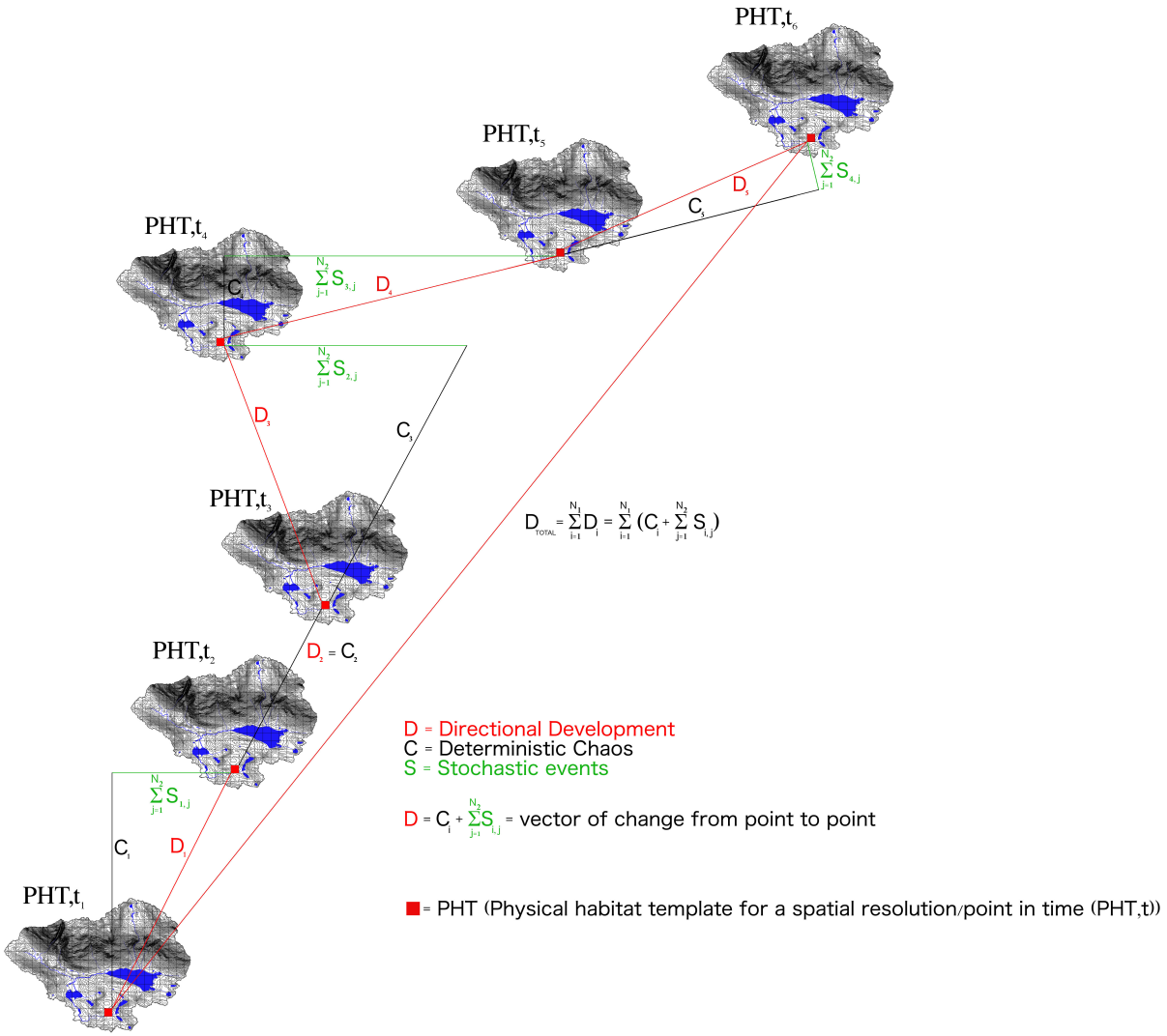

Figure 2.12: Framework for understanding the directional development of the physical habitat template (PHT) over time.

2.5 Conclusion

The general synthesis here will contribute to a better understanding of spatiotemporal patterns and processes. Space-for-time substitution makes the assumption that the spatial and temporal variation is equivalent (Pickett 1989). These results show this is not the case and that the initial state exerts control on watershed development, even with only five streams analyzed. Time still continuously affect the watershed and are significantly correlated with the stream network development. The data presented and the conceptual model show that the initial space set by the PHT can provide valuable information on the rate of change from processes within. This approach can facilitate better insights into modeling hydrology, biotic assemblies and stream community. Development of a universal physical habitat template on a watershed scale should be considered to help compare fields of research and among landscape regions. Additional research is warranted to grasp the change and succession process with time, which again can help explain nutrient exchange, habitat utilization and species and populations migration patterns. The conceptual model presented here with the use of PHT creates a more holistic understanding of the interconnectedness within a watershed and the stream system. The conceptual model should be applied with continuous remote sensing and a large set of variables to understand the processes and patterns with time, for instance changes and fluxes within a year. New technology and more accurate remote sensing technology contribute to a better understanding and quantification of both abiotic and biotic morphological factors related to streams and watersheds, and will simplify the process of creating a more accurate PHT in the future. These findings have implications for biodiversity conservation and management, and could provide insights into processes and changes in communities due to initial factors and random events influencing both process and patterns. The space-time continuum of landscapes are here suggested to be controlled by deterministic chaos due to the physical habitat template present at a specific point in time, since a past biosphere does not exist separately from a biosphere of the present (Rull 2014). The physical habitat template is

continuously influenced through the presence a “noise” in form of stochastic events, the unseen chaos. Establishing a PHT in a fourth-dimensional space provides a solid background for all ecological interactions and makes it easier to understand population colonization and distribution. Time as a fourth dimension adds the possibility to analyze the PHT development rate as well as the different individual layers. A recommendation here is thus to use a scaled PHT to help expand the knowledge on change and development of physical habitats, and should be included in future sustainability river management, habitat restoration and fisheries management.

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2.7 Morphometric factors

Median elevation

Horton (1932) thought that median elevation would be a better indicator of various hydrological conditions than the mean elevation, like mean temperature and snow cover. Results show that the median do differentiate more between our watersheds, and could therefore explain more of the landscape differences.

Form factor

Form factor is the ratio of the width (A) to the length (Lb) of the drainage watershed.
This factor is indicative of the flood regime of the watershed stream. However, watersheds of irregular form and especially permeable soils form factor will not be a sensitive indicator of hydrologic characteristics (Horton 1932).

Elongation rato

Shape is here expressed as the ratio between the diameter of a circle with the same area as the watershed and the maximum length of the watershed (SCHUMM 1956).

Circularity ratio (Rc)

The ratio of the watershed area to the area of a circle with the same perimeter (Miller 1953).

Drainage density

Drainage density is the amount of stream channel length per unit area and an excellent indicator of surface permeability of a watershed. Ranging form 1.5 – 2.0 for steep, impervious watersheds with high precipitation, down to zero or close to zero for watersheds with permeable surfaces where precipitation ordinarily is taken into the soil through infiltration (Horton 1932).

Length of overland flow

Length of overland flow is the distance of overland travel of water before reaching definite stream channels, and is of great importance hydrologically, especially to flood intensity from small areas (Horton 1932).

Stream frequency

This ratio was calculated in Grass, and is the number of streams per unit area.

Mean bifurcation ratio (Rb)

Mean bifurcation ratio is the mean of the bifurcation ratio for each stream order, where bifurcation ratio is the ratio of the number of streams of the next highest order (Horton 1945).

Compactness

This ratio was calculated in Grass, and is expressed as the ratio between the perimeter of the watershed and that of a circle of equal area.

Relief ratio (Rl)

Relative relief expressed as the height of the watershed divided by its length (SCHUMM 1956).

Melton ruggedness number

Melton (1965) characterized the ruggedness of a basin Ruggedness of a watershed as the hight between the maximum and minimum elevation of the watershed on the area squared.
Very rugged are the relative relief number could theoretically vary from 0 to a large number, in general very rugged area could have a high relief number as 2.0 or 3.0 for a first order basin, but rarely exceeds 1.0 for a third and forth order basin.

Fitness ratio

The ratio of stream channel length to the watershed perimeter is a dimensionless measure of fitness of topographic texture relative to watershed size (Melton 1957).

Length area relation

Length area relation, or the rate at which a watershed area increases in a downstream direction are important factor affecting the longitudinal profile (Hack 1957).

3: Diet of juvenile coho salmon and Dolly Varden in streams of different age since deglaciation in Glacier Bay National Park, Alaska.

Abstract

Sympatric stream dwelling juvenile coho salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*) were studied in five streams of different complexities across a gradient of 39 to 206 years following glacial retreat. Contribution of stream, terrestrial and marine source items to the diets were assessed for each species, as well as diet niche breadth and diet overlap in the context of stream age and development. Percent utilization of prey between the streams was different in food sources from aquatic (AFS), terrestrial (TFS) and marine (MFS), and was related to abundance of prey items in each species foraging zone and individual feeding behavior. Significant overlap in diet between juvenile coho salmon and Dolly Varden was found for all streams except Berg Bay South Stream (BBS), and was independent of stream age. Niche breadth increased with increased TFS for both species. Increased fork length (FL) of both species was linked with greater AFS and decreased FL for both species associated with increased TFS, suggesting the increase in niche breadth was due to resource depression. MFS for both juvenile coho salmon and Dolly Varden was related to pink salmon spawning abundance and higher presence in odd years. For juvenile Dolly Varden more benthic items were consumed while juvenile coho salmon consumed more drift and terrestrial taxa. Chironomidae (larvae, pupae and exuviae) were the most abundant prey in the diet of both species (> 50%) of AFS abundance except for BBS. Despite this, the Odds ratio indicated Chironomidae were negatively selected in relation to their high abundance in the benthos for both juveniles species in all streams except Ice Valley Stream (IVS). All other aquatic prey items were positively selected compared to their presence in the benthos. These findings indicate juvenile coho salmon and juvenile Dolly Varden are able to coexist together, and the change in diet overlap and niche breadth is a result of the foraging zone used and food depression, rather than a change in prey community.

3.1 Introduction

Juvenile coho salmon and Dolly Varden inhabit the same streams in deglaciated watersheds in Glacier Bay, where development and succession of communities can be studied over a chronosequence of 250 years. Flexibility in the foraging behavior of fish is an important adaptive feature, as most natural environments will wary both spatially and temporally (Dill 1983). This flexibility will therefore be influenced by a potential change in population dynamics and abundance of potential prey items with stream age. Milner et al. (2000) observed a significant increase of microcrustacean and macroinvertebrate taxa, as well as juvenile salmonid abundance and diversity in older streams. Flory and Milner (2000) found colonization of new invertebrate taxa to be influenced by the development of riparian vegetation and increasing stream summer water temperatures. Milner et al. (2000) found colonization of fish communities (abundance and diversity) to be strongly related to stream age, primarily governed by water temperature, sediment loading and stream discharge (Milner and Bailey 1989). Stonefly Creek (SFC), the youngest study stream was colonized by pink salmon (*Oncorhynchus gorbuscha*) and Dolly Varden within 10 years after stream formation, followed by sockeye salmon (*Oncorhynchus nerka*) and coho salmon (Milner et al. 2011). Chironomidae is typically the first macoinvertebrate colonizing taxa followed by Ephemeroptera and Plecoptera (Milner 1987, Milner 1994).

Over time biotic controls become more important with vegetational bank stabilization and coarse woody debris (CWD) contribution playing a major role in juvenile fish populations (Milner et al. 2000). Riparian vegetation could exceed 90% within 50 years in absence of flood-plain inundation or channel migration (Milner and Gloyne-Phillips 2005). Piccolo and Wipfli (2002) found that alder dominated sites export significantly greater amounts of invertebrates from headwater streams to downstream habitat compared to conifer dominated sites, and therefore are integral to the vitality of the stream network (Wipfli et al. 2007). Riparian vegetation could also facilitate colonization of Trichoptera and Chironomidae into

the macroinvertebrate community (Milner et al. 2008). Wipfli and Musslewhite (2004) found aquatic taxa to significantly respond to the red alder density gradient. Fish-less headwater streams are therefore inseparable from downstream fish populations (Naiman and Latterell 2005). An increase of (CWD) with watershed development also influences fish behavior, as woody debris is frequently used as cover by juvenile coho salmon and Dolly Varden (Dolloff and Reeves 1990). Milner et al. (2000) found microcrustacean diversity, a potential prey item, to be related to amount of CWD and pool habitat, while macroinvertebrate taxa to be related to bed stability, amount of CWD and pool habitat.

Juvenile coho salmon and Dolly Varden are the most common in-stream salmonids in Glacier Bay watersheds. Dolly Varden are typically the first salmonid to colonize new streams following deglaciation (Milner and Bailey 1989), and Pess (2009) found that coho salmon could establish a viable population within few years of initial colonization. Links between the main stream channel and small tributaries are important, as coho salmon and Dolly Varden spawn, rear and overwinter in second order tributes (Bramblett et al. 2002). Dolloff and Reeves (1990) found an increase in water depth, focal point depth and distance to nearest fish with increasing fish size, whereas the distance to nearest cover decreased. Ontogenetic shifts in diet within fishes are almost universal (Werner and Gilliam 1984), and selectivity can occur when the relative frequency of prey items in a predator differ from the relative frequency in the environment (Chesson 1978).

Juvenile coho salmon are opportunistic predators (Nielsen 1992), and a typical drift feeder (Nakano and Kaeriyama 1995), occupying and defending midwater positions (Dolloff and Reeves 1990). Juvenile coho salmon are aggressive and territorial (Chapman 1962), and territory sizes inversely relate to the density of benthic food (Dill et al. 1981). Johnson and Ringler (1980) found juvenile coho diet to be closely associated with drift, and to feed heavily on terrestrial invertebrates from June through September. Coho salmon nomads could be a substantial part of the total watershed coho salmon production, and might affect both natal

and non-natal streams. Several studies indicate the nomads lifecycle to include spring/summer estuary rearing as 0+ and then overwintering in freshwater habitats (Koski 2009). Juvenile Dolly Varden, compared to juvenile coho salmon, is typically a bottom dweller and seldom territorial (Dolloff and Reeves 1990). The Dolly Varden life cycle is complex and may vary from anadromous life histories to stream resident life histories. Kishi and Maekawa (2003) found some stream-resident Dolly Varden physiologically preserved the potential ability to smolt, even without expressing an anadromous life history. Occurrence of variances in juvenile coho salmon and Dolly Varden migration could therefore create a larger variation in or between population abundance and FL.

Returning adult salmonids transport marine nutrients to their natal stream, and these accumulated marine derived nutrients (MDN) become incorporated into multiple trophic levels, and help sustain the productivity of freshwater food webs (Chaloner and Wipfli 2002). Bilby et al. (1998) observed increased densities and improved condition factors, and (Wipfli et al. 2003, Giannico and Hinch 2007, Kiffney et al. 2014) found an increase in juvenile coho growth with addition of salmon carcasses. Kiffney et al. (2014) found additions of salmon material in experimental channels to result in a strong bottom-up effect on selected invertebrates, increasing Chironomidae biomass. Nakano and Kaeriyama (1995) found Chironomidae larvae to be the most abundant prey in both juvenile coho salmon and Dolly Varden. Most taxa persisted within the community following colonization, with the exception of cold temperature tolerant first colonizers, but with a marked change in relative abundance (Milner et al. 2008). Salmonid spawning redds may also facilitate the persistence of some early colonizers (e.g. Simuliidae) due to disturbed patches (Milner et al. 2008, Monaghan and Milner 2008).

Life histories, and migration differences could affect the foraging. Mason (1976) found supplemental feeding of juvenile coho salmon to cancel out density effects on survival and outmigration, while accelerating growth rate and substantially increasing the lipid reserve.

Low food availability should lead to a response from fish, and alter their behavior to ensure higher feeding rates, larger territories and broader diets (Dill 1983). The effect on the community and processes in ecosystems are however poorly understood (Post et al. 2008). Variations between stream to ocean migration, might also be a result of lower food availability, or possibly an adapted foraging behavior. Estuary juvenile coho salmon have been shown to be a substantial component of total watershed production (Koski 2009). These fish could also affect the variation of population diet and growth, with occurrence of migration between the estuary and up-stream, as movement impact predator diet (Polis et al. 1997).

The overall aim of this study was to examine the diet of juvenile coho salmon and Dolly Varden to ascertain if differences occurred between species according to the ages and complexity of the watershed within Glacier Bay. The following hypotheses were tested;

Hypothesis 1: Juvenile coho salmon will utilize drifting invertebrates more than juvenile Dolly Varden, due to their feeding preferences.
Hypothesis 2: The incidence of terrestrial derived food source (TFS) will increase in the diet of both juvenile coho salmon and Dolly Varden in older streams due to increased growth of riparian vegetation.
Hypothesis 3: Diet niche breadth of both juvenile coho salmon and juvenile Dolly Varden will increase with stream age due to increased TFS.
Hypothesis 4: The amount of overlap in the diet between juvenile coho salmon and Dolly Varden will decrease as the amount of TFS increases.
Hypothesis 5: The amount of overlap in the diet between juvenile coho salmon and Dolly Varden will decrease the mean juvenile FL.
Hypothesis 6: Amount of aquatic derived food source (AFS) influences the mean juvenile FL.

3.2 Methods

3.2.1 Study area

Five study streams are located temporally in a young chronosequence following deglaciation in Glacier Bay, Alaska (Figure 3.1). Glacier Bay is located in a temperate rainforest region and consists of two major fjord arms. The Chronosequence study streams are aged from 39 year to 206 years; Stonefly Creek (SFC), Wolf Point Creek (WPC), Ice Valley Stream (IVS), Berg Bay South Stream (BBS), and Rush Point Creek, (RPC). Stream ages were determined by use of historical, satellite and aerial photographs, journal articles and unpublished data. Stream age of SFC was determined by the year the stream mouth was uncovered from under the ice. Other information is from (Milner et al. 2000). Selection of stream reach for sampling was selected based on earlier studies (Sønderland and Milner).

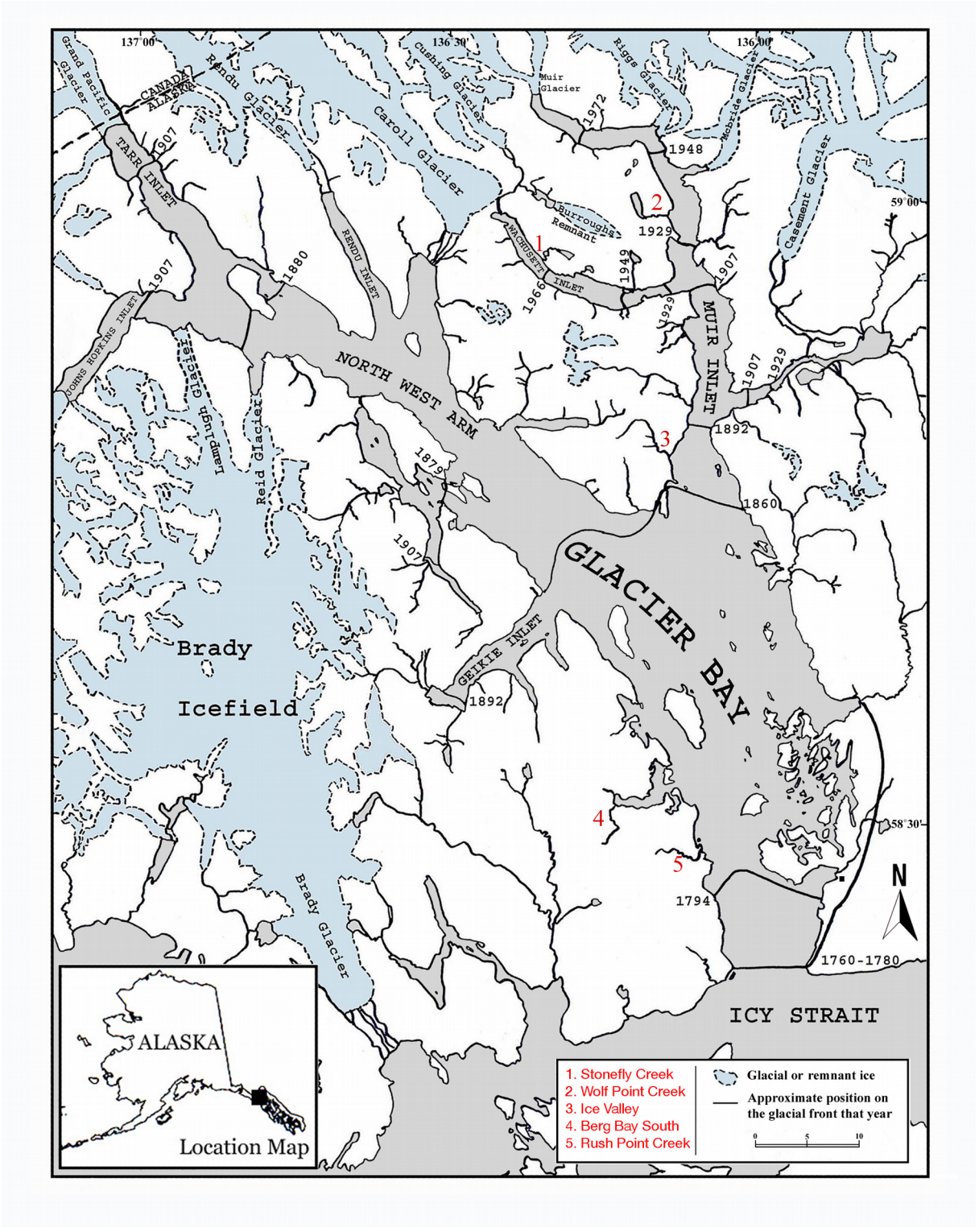

Figure 3.1 Study stream locations.

3.2.2 Sampling

Juveniles were captured in minnow traps (400mm x 220mm, with a 6mm mesh) that were deployed for approximately 1,5 hours. Traps were baited with fish eggs treated with Bengals Iodide for 30 minutes and placed into Whirl-Pak bags in 2009 and 2010, while using Kinder Egg containers to avoid consummation eggs by trapped fish in 2011. Juvenile fish were sedated with clove oil before FL was measured gut content was evacuated using a syringe filled with stream water and a feeding needle attached (Meehan and Miller 1978). Juveniles were placed in trays with stream water to recover before being released back into the stream. No mortality occurred. Evacuated content were preserved in 70% ethanol, and analyzed under a stereo microscope.

Three Surber samples (0.93 m^2 with a 330lm mesh size net) were collected from each stream study reach to assess the difference in utilization of the benthic prey groups available in the stream, as used in previous studies (Milner and Bailey 1989, Milner 1994). Surber samples were stored in Whirl-Pak bags with 70% ethanol until sorted in the lab under a stereomicroscope. Algae, plant fragments and exuviae present in the Surber samples were not enumerated, although these items were present in the diet. Macroinvertebrates and dietary items were counted under the microscope, where only larger parts like heads and larger body parts were counted to make sure dietary items only were counted once, and therefore would be an underestimate instead of an overestimate. Strongly decomposed items and parts are not used in the calculations. Due to the variation in diet and source, only the main prey groups utilized >10% in one stream or more were used. The rest were grouped together before being used in the statistics (Appendix 2). Other Diptera larvae, pupae and exuviae were grouped in other Diptera to lower the number of groups even though they were all >10%. Sand grains, plant fragments and extra wings, eggs and unidentified material were not analyzed further (Appendix 2). However, only sand grains and plant fragments were found in large quantities.

No biomass calculations have been undertaken, thus species size and size variation among the same species are not accounted for.

3.2.3 Statistics

Statistics were done using the statistical software environment "R", version 3.1.2 (GUI 1.65). Principal component analysis (PCA) was then calculated to assess the directional relationship between the percent TFS, AFS, MFS items per fish and empty guts per fish, niche breadth, diet overlap and mean juvenile salmonid FL.

Niche breadth was calculated accordingly to (Levins 1968) index based on the juveniles utilization of diet items, then (Hurlbert 1978) standardized niche breadth was calculated. This were done to distinguish differences in juveniles food resources use with stream age.

$$\hat{B} = \frac{1}{\sum \hat{P}_j^2} \qquad \hat{B}_A = \frac{\hat{B} - 1}{n - 1}$$

$\hat{B}$ = Levin's measure of niche breadth

$\hat{P}_j$ = Proportion utilized prey j as diet

$\hat{B}_A$ = Hurlbert standardized niche breadth

Niche breadth is equal to 1 if only one prey item is exploited, and highest niche breadth occur when all the different prey items are exploited equally.

To evaluate overlap between juvenile coho salmon and Dolly Varden, Morisita's similarity index was used (Morisita 1959) which has been shown to be minimize bias (Smith and Zaret 1982).

$$\hat{C} = \frac{2 * \sum_{i}^{n} \hat{P}_{ij} * \hat{P}_{ik}}{\sum_{i}^{n} \hat{P}_{ij} * [(n_{ij} - 1)/(N_j - 1)] + \sum_{i}^{n} \hat{P}_{ik} * [(n_{ik} - 1)/(N_k - 1)]}$$

$\hat{C}$ = Niche overlap between species j and k.

$\hat{P}_{ij}$ = Proportion of diet item i of the total items found in the diet of species j.

$\hat{P}_{ik}$ = Proportion of diet item i of the total items found in the diet of species k.

n_{ij} = Number of individuals of species j with i in the diet.

n_{ik} = Number of individuals of species k with i in the diet.

N_j, N_k = Total number of prey items in the diet of fish species j and k.

$\hat{C}$ varies from 0 to 1 from species that have no prey items in common to prey items proportions being identical. $\hat{C}$ larger ≥ 0.60 suggests significant overlap (Zaret and Rand 1971).

Odds ratio was calculated to assess the selection of prey by juvenile coho salmon and juvenile Dolly Varden in relation to abundance in the benthos (Gabriel 1978). Values of this selectivity index ranges from zero to infinity, indicating a positive or negative prey selection.

$$L = \ln\left[\frac{(p_1 q_2)}{(p_2 q_1)}\right]$$

L = Log of the odds ratio

p_1 = percentage of diet of a given prey item

q_1 = percentage of diet of all other prey items

p_2 = percentage of food item in the environment

q_2 = percentage of all other food item in the environment

Contribution of AFS, TFS and MFS were assessed by the percentage of prey items found to minimize the effect of specialization and juveniles with empty guts, and placed in pie diagrams of percentage of AFS, TFS and MFS found per stream for juvenile coho salmon and Dolly Varden. Regression was used to understand the effect of different environments contribution on mean FL. To help understand the difference in food preferences, fish that utilized AFS, TFS and MFS were calculated. The amount of AFS, TFS and MFS per fish were on the other hand calculated for all three years to see if there might be a yearly variations. Each group were put together into graphs to visualize the difference in group prey abundance between juvenile coho salmon and Dolly Varden.

3.3 Results

During the summer season of 2009 to 2011 the stomach content of 436 juvenile coho salmon and 330 Dolly Varden were examined. Nine juvenile coho salmon had empty stomachs, 8 from 2011 whereas 26 juvenile Dolly Varden had empty stomachs, 12 from 2011. Juvenile coho salmon 0+ were most commonly observed in mid section of the water column of pools, and tributaries, while 0+ juvenile Dolly Varden were most common under cover and in smaller tributaries, otherwise more evenly spread out on the bottom of the steam. Both species 1+ and 2+ fish were common in faster flowing water, especially behind larger substrate. Juvenile coho salmon and Dolly Varden were found to consume a wide range of prey items, and smaller individuals consumed smaller prey items. Large amounts of exuviae were found in the diet of both juvenile coho salmon and Dolly Varden. Specialization on specific prey items was observed among both juvenile coho salmon and Dolly Varden.

Chironomidae, Simuliidae and Ceratopogonidae dominated the benthos in SFC and WPC, with the abundance of almost 30 000 Chironomidae per m^2 in SFC. Plecoptera were more common in the older streams BBS and RPC. Ephemeroptera were also abundant in the benthos of SFC, BBS and RPC. Juvenile coho salmon and Dolly Varden showed a negative selection for Chironomidae larvae, except in IVS, while all other taxa are positively selected compared to their abundance in the benthos. Juvenile Dolly Varden showed a higher selection for Ephemeroptera and Plecoptera than juvenile coho salmon in all streams, except for BBS (Table 3.1). The diet juvenile coho salmon contained more TFS than juvenile Dolly Varden, and Hydrachnidae nymphs and Crustacea from the drift. Dolly Varden diet contained more benthic prey, and utilize more exuviae than juvenile coho salmon (Figure 3.2, 3.3 and 3.4).

Chironomidae made up the largest proportion of the AFS component in the diets of juvenile coho salmon and Dolly Varden, ranging from 55 to 89%. The only exception was BBS, where the largest fraction (50%) in juvenile coho diet was Hydrachnidae nymphs. Total AFS in the

diets of juvenile coho salmon in all streams ranged between 66.4 to 91.3%, and juvenile Dolly Varden ranged between 83.0 to 98.2% (Figure 3.5 a) and b)). TFS for juvenile coho salmon ranged from 6.2 to 33.6%, and juvenile Dolly Varden ranged between 0.8 to 8.6% (Figure 3.6 a) and b)). TFS in IVS for juvenile coho salmon was > 30% of the total diet, while only 1.8% of the total diet of juvenile Dolly Varden. Juvenile mean fork length (FL) was higher with increased percent AFS items, while mean FL decreased with increasing percent TFS items in the diet (Figure 3.7 and 3.8).

AFS utilization by juvenile coho salmon and Dolly Varden was similar across the study streams; 93.90% to 98.88% and 85.42% to 97.83% respectively. Chironomidae was utilized >65% by juvenile coho salmon and Dolly Varden. WPC was the only stream where < 60% of juvenile coho salmon had consumed TFS, whereas juvenile Dolly Varden in all streams consumed < 45% TFS (Figure 3.9).

Niche breadth was largest in IVS, SFC and BBS for juvenile coho salmon and SFC, BBS, IVS for juvenile Dolly Varden. There was a difference in species taxa found between the different streams, however the Morisitas overlap index was significant for all streams except BBS (0.56), even with the variation in AFS, TFS and MFS across the chronosequence. Juvenile coho salmon in WPC had the lowest percent TFS items for both species and showed the highest diet overlap (0.91). Juvenile salmonids in streams with high niche breadth had the lowest diet overlap, except for SFC, which had larger niche breadth and still a high overlap (Table 3.2). Directional relationships are found in the PCA loading plot, showing the relationship between percentage of AFS, TFS, MFS per fish, FL length for both species and diet overlap (Figure 3.10).

Mean diet composition AFS, TFS and MFS per fish is similar from year to year. Sample dates, the number of fish that were evacuated for gut content and their FL are linked together (Figure 3.11a) and b)). The odd years show more MFS and empty guts, and have sea lice present in

the two oldest streams. No juvenile coho salmon had empty guts in 2010, and juvenile Dolly Varden had empty guts only in SFC and BBS. There were low numbers of gut evacuated in WPC and IVS in 2010 and in BBS in 2009 for juvenile Dolly Varden. Percentage of MFS items per fish is similar for both species, while more juvenile Dolly Varden has utilized this food source.

3.4 Discussion

3.4.1 Environment impact

Juvenile coho salmon consumed more terrestrial and drifting organisms, while juvenile Dolly Varden consumed a greater amount of aquatic benthic food sources, similar to the findings of (Nakano and Kaeriyama 1995) thereby supporting Hypothesis 1. Change in stream age and in stream community did not seem to influence diet niche breadth or diet overlap between the two species. This suggests dietary differences between the two species to be related to foraging zones where dietary differences partly are results of differences in foraging behavior traits, and corresponds with observations by (Nakano and Kaeriyama 1995). This study shows percent AFS items to be more important then percent TFS, and that in comparison more TFS caused lower fish growth. In a study conducted from April to October Wipfli (1997) found aquatic derived invertebrates and terrestrial derived invertebrates to be equally important as prey. However this was during summer when terrestrial invertebrates has been found to primarily occur and when aquatic invertebrate biomass are nearly at their lowest (Nakano and Murakami 2001). Utilization of terrestrial food source was linked to lower *in-situ* aquatic availability, leading to resource depression. Pink salmon spawner provided more MFS in odd years, as odd year support greater returns of pink salmon (Milner and Bailey 1989). Data presented here can only show the difference of utilization of prey between the juvenile coho and Dolly Varden among the five study streams at the time of sampling. Changes in food availability are often unpredictable and influence each species differently, and may lead to a

constantly change in the stream fishes' competitive environment (Angermeier 1985). There will be seasonal variations in and among the streams, but how much this affects juvenile foraging of these two species is unknown. These data imply similar diet utilization by juvenile coho salmon and Dolly Varden between streams and by year. These data were from the beginning of the pink salmon run, and further studies later in the fall would improve the understanding of the importance, and possibly shift, in diet due to salmon runs.

3.4.2 Aquatic input

The mean FL of both species was influenced by percent AFS items in the diet, significantly so for juvenile coho salmon. There was a change in species composition of each taxa group with stream age, but no change the in diet niche breadth or diet overlap between juvenile coho salmon and Dolly Varden was connected to stream age, except for Ephemeroptera. Milner et al. (2000) found the percentage of Ephemeroptera in benthic stream communities to increase significantly with stream age and amount of CWD. Ephemeroptera was found to increase with stream age in the diet of juvenile coho salmon, while decreasing in the juvenile Dolly Varden diet. Most likely due to an observed change in the taxa composition of Ephemeroptera, which could relate to the habitat utilizations of relevant Ephemeroptera taxa, and that these conform with the juvenile foraging zone. Percent of AFS items in the diet of juvenile coho salmon and Dolly Varden show a directional relationship with mean FL. There is a decrease of AFS prey abundance in juvenile Dolly Varden diet with stream age, which could be due to the large differences in prey availability from the younger streams, and foraging behavior of juvenile Dolly Varden. Almost 30 000 Chironomidae per m^2 were found in SFC, and this abundance would be expected to be reflected in the salmonids' diet. The negative selection of Chironomidae in the diet compared to their abundance in the benthos follows similar patterns to those found in WPC by Milner (1994). Chironomidae larvae were typically the most abundant prey for both juvenile coho salmon and Dolly Varden, as found by Nakano and Kaeriyama (1995). Kiffney et al. (2014) linked faster growth of juvenile fish to chironomid

abundance, as this is the largest group in AFS for most streams, except for BBS. While more juvenile coho salmon utilized AFS compared to juvenile Dolly Varden and could be due to chironomid in drift, as the greater AFS in juvenile Dolly Varden. The largest percent AFS items for juvenile Dolly Varden was found in IVS, which has the lowest percent AFS items and highest percent TFS items for juvenile coho salmon. Simuliidae showed a clear negative trend in diet selection of both species, from younger to older streams, due to greater abundance of Simuliidae in younger streams.

3.4.3 Terrestrial input

The occurrence of TFS did not increase in older streams due to increased growth of riparian vegetation, thereby disproving Hypothesis 2. Allan et al. (2003) found higher biomass of terrestrial invertebrates under deciduous compared to conifer plants, but no significant difference in terrestrial derived invertebrates in juvenile coho salmon diet associated with change in location plant or forest type. These findings support this study, as no direct relationship has been found with stream age which affects forest type present. Riparian vegetation is suggested to influence the terrestrial invertebrate input (Wipfli 1997). In stream macroinvertebrate samples also contained TFS, in particular Hymenoptera, exceeding >14 per m^2 in SFC and RPC. Coleoptera, Hemiptera and Collembola were also present in some streams, suggesting some of the TFS in Dolly Varden could come from the benthos. TFS in the diet per juvenile coho salmon and Dolly Varden was highest IVS and BBS.

3.4.4 Marine input

MFS is utilized relatively equally between juvenile coho salmon and Dolly Varden, and was directly linked to the presence of pink salmon spawners. Anadromous salmonids represent a major vector for marine nutrient across environments (Cederholm et al. 1999). Juvenile Dolly Varden percent MFS utilization is higher compared to percent TFS utilization in WPC, BBS and RPC, due to higher pink salmon abundance. The percentage MFS per fish was higher in odd years, except for juvenile Dolly Varden in SFC. Higher numbers of empty guts were evident in odd years, except for juvenile Dolly Varden in BBS 2010. Percentage of empty guts per juvenile salmonid follows percent MFS per fish and stream age in PCA space, possibly due to a shift in diet towards MFS due to their digestive flexibility (Armstrong and Bond 2013). The lower densities of juvenile Dolly Varden in even years, could be due to the lower pink salmon spawning, as juvenile Dolly Varden could return upstream with returning pink salmon to specifically prey upon fish eggs and carcasses. The percent MFS items per stream should have been higher as salmon eggs were commonly preyed upon by both species, and salmonids is strongly attracted to eggs (Quinn et al. 2012), but not counted in 2009 and 2010, and therefore not included in the three year environment contribution. Sea lice (*Lepeophtheirus salmonis*) was only found in the two oldest streams, and was found in RPC in 2011 to contribute more sea lice than eggs to the diet.

3.4.5 Niche breadth

Diet niche breadth of both juvenile coho salmon and Dolly Varden did not increase with stream age but increased with increased of TFS, partly supporting Hypothesis 3. Niche breadth showed a directional relationship with the percent TFS items per fish for both juvenile coho salmon and Dolly Varden in PCA space, indicating increased TFS causes a change in niche breadth. There are only smaller variations in niche breadth between streams, except for juvenile Dolly Varden in RPC, where lower niche breadth could be due to a large fraction of

plant material present in the diet, which is excluded in these calculations. SFC has the highest niche breadth for juvenile Dolly Varden, and could be linked to the amount of deciduous vegetation. Diet niche breadth increased with TFS for both juvenile coho salmon and Dolly Varden, and was highest in IVS, SFC and BBS. Angermeier (1982) found increases in fish diet breadths for all species as food resources declined, suggesting resource depression. The differences in spatial subsidies use will also be related to yearly fluctuations, as (Nakano and Murakami 2001) found aquatic insect emergence to peak in spring, when terrestrial biomass was low, and terrestrial input occurred primarily in the summer, when aquatic biomass was at its lowest. This is likely the case for IVS and BBS, streams with lower mean FL length. IVS is the stream with the largest difference in utilization of AFS and TFS between juvenile coho and Dolly Varden, and the only stream where odds ratio for Chironomidae was positive. Erős et al. (2012) found growth to be highest in spring, reduced in the summer when the terrestrial invertebrate influx was greatest and aquatic invertebrates availability was low and a slight increase again in autumn for brown trout (*Salmo trutta*). While only sampling early fall, the FL relation to terrestrial invertebrates is negative, and the subsidies dynamic could be explained by lower *in-situ* stream food availability. Nutrient contribution from reciprocal subsidies could be larger in streams with anadromous salmonids due high contribution.

3.4.6 Diet overlap

The amount of overlap shows similar direction as percent AFS per juvenile in PCA space, while overlap decreases with increasing TFS per stream, supporting Hypothesis 4. The increased overlap increased juvenile FL thereby disproving Hypothesis 5. There was a difference in abundance and number of prey groups between streams, but the diet overlap was rather consistent. These results follow the findings of Nakano and Kaeriyama (1995), suggesting genetic behavior traits regarding foraging and foraging zones. The Odds Ratio also indicated that utilization of prey groups from the benthos was similar between streams. Less overlap between juvenile coho salmon and Dolly Varden and an increase in niche breadth seem to be driven by food availability in the foraging zone. The higher overlap and larger FL also suggest higher food abundance or energy input. The only stream, BBS, with no significant overlap, was a result of low food abundance. Diet overlap between sizes must be analyzed by species or by biomass, as there is overlap between sizes. The link between FL and overlap and the difference in Odds ratio suggests a response to lower food abundance. Lower overlap in BBS could also be due to the high consumption of Hydrachnidae nymphs, where it accounts for almost half the AFS in the diet of juvenile coho salmon, with an abundance of 15 to 1 compared to juvenile Dolly Varden. This large difference could be a result of juvenile coho salmon being typical drift feeders (Nakano and Kaeriyama 1995), and that the coho salmon FL length was the lowest in BBS. Hydrachnidae nymphs were found to both be free swimming but also attached to other macroinvertebrates and adult Diptera. Most Hydrachnidae nymphs found were not attached, while some could have been dislodged from the parasitized host. Diet of juvenile sockeye salmon (*Oncorhynchus nerka*) in SFC from 2004 shows a strong utilization of Hydrachnidae nymphs in their diet among different groups of Crustacea, and would target these free swimming Hydrachnidae nymphs in the Kettle Lake. Low abundance Hydrachnidae nymphs and Crustacea in the diet of juvenile Dolly Varden compared to juvenile coho salmon suggests utilization of drift by juvenile coho salmon, again supporting Hypothesis 1.

3.4.7 Foraging

Juvenile coho salmon and Dolly Varden were found to consume input from the surrounding environments. Individual specialization was found when analyzing the stomach samples, suggesting a direct choice of prey. The youngest stream, SFC, had the highest percentage of AFS diet items for coho and no empty guts. Juvenile Dolly Varden in SFC had higher percent TFS items, and was the stream where juvenile Dolly Varden had 8 empty guts. Empty guts and specialization could skew the population resource use some when calculating per fish. By using the total percent items found, a more strong pattern emerged. Individual strategy, which specialization can be seen as, and their optimal strategy will be conditional upon specific priorities and constraints for any given individual (Le V. Dit Durell 2000). Individual prey selections were found for both species, but for the populations, as a whole the overall change in diet came from changes in abundance of prey in each of the foraging zones for each species. Devictor et al. (2010) showed specialization to be intrinsically linked to niche breadth, which help explain higher niche breadth in SFC. Years and streams with low juvenile Dolly Varden diet samples could therefore skew their niche breadth some. Smaller sized juveniles consumed smaller sized prey, however most often in the same prey group. Keeley and Grant (2001) found the mean range of prey size eaten generally to be within the hypothesized constraints of gill-raker spacing and mouth size. This could also lead to a differences in prey items among the same species, due to the difference in juvenile size, like the higher abundance of Hydrachnidae nymphs in BBS which had the lowest juvenile coho salmon FL. However this is likely due to food depression, as BBS and IVS had the highest amount of TFS per juvenile coho salmon and Dolly Varden, and corresponding lowest FL. This behavior will also be dependent on what prey items which are present in the foraging zone of the fish. Juvenile coho salmon and Dolly Varden movement influence their diet, as predator abundance usually is enhanced by prey subsidies beyond the supporting local resources due to movement of either prey or predator (Polis et al. 1997). The amount of in-stream, or even transverse stream migration is unknown, but diet samples will reflect what has

been consumed recently. These findings support (Bilby et al. 1998) who also found plant fragments and sand grains in the diet. Dolly Varden had large amounts of plant material in their guts, like moss, lichens, roots, seeds and other plant fragment from grass, and other plant stems, likely from the semi-aquatic environment. Sand grains were counted only when separated from parts of egg consumption and macro-invertebrate housing, and would therefore be a strong underestimate. Sand grains were mostly larger sand grains comprised of quartz, often with inclusion of biotite. The decision to either swallow or reject potential food items might seem random, but larger sized sand grains and plant materials were observed rejected in the field, while smaller sized items were swallowed. This could suggest that the larger size items more easily could be recognized by the juvenile salmonids as possible food items. Since only heads and larger parts were counted, dietary findings were likely underestimated, except for the possibility of juveniles consuming parts of the items among several juveniles, which was observed during competition among juveniles for the same prey. This is only likely for larger macro-invertebrates and dietary items like Coleoptera, Trichoptera and Araneae. Competition for prey in juvenile coho salmon in particular was observed. This could account for different larger parts of Coleoptera or Diptera in the stomach of various fishes. Half consumed items and lots of smaller parts can also drift downwards or get stuck in the benthic. This could lead to an overestimate of these prey groups, but there would be a strong underestimate to begin with. Exuviae was found to be be an important part of the diet for both juvenile coho salmon and Dolly Varden. Exuviae of Chironomidae and Simuliidae sometimes had to be directly targeted, and are likely to be found in high numbers both in the drift and in the benthos. Mason (1976) found that juvenile coho salmon growth and biomass yield of unfed populations were negatively related to population density, and (Dill et al. 1981) found territory size to be inversely related to territory benthic food density. Physical habitat, its processes and prey abundance, will control their abundance. If collection was executed several times during the year, we would better understand the difference in diet between the in-stream juveniles, and get a better understanding of ontogenetic shifts in diet and changes in abundance of input categories.

3.5 Conclusion

The extensive dataset has provided insight in the diet of common sympatric juvenile coho salmon and Dolly Varden over a chronosequence of around 250 years in Glacier Bay, demonstrating negligible change in diet overlap temporally between the two species, and no relation to change in niche breadth. Larger diet niche breadth, lower diet overlap and higher percentage of TFS items per fish indicate resource depression. The diet of juvenile coho salmon and Dolly Varden is likely a direct function of genetic foraging behavior and stream prey abundance, rather than a change in prey selection or prey community. Since percent AFS items positively influenced the growth of both juvenile species and percent TFS items in the diet influence growth negatively, the effect of cross boundary subsidies will have a larger impact in streams with low *in-situ* stream production. Addition of analysis of biomass and energy provided by prey items could improve the understanding of feeding behavior and possible selection with spatial and temporal variation. Further research is warranted to assess the yearly variations, specialization and the ontogenetic shift in diet. Individual selections of specific prey items are also important to further the understanding of the diets of juvenile salmonids, as this seems to be a choice taken by the individual salmonids, rather than an effect of competition. These findings will help stream management in understanding of the importance of AFS, TFS and MFS and how these change depending on the stream *in-situ* production. The physical foraging zone and physical habitat were the most important factors for these two salmonid populations in Glacier Bay, southeast Alaska, and will most likely be the same anywhere in the world for these two sympatric species.

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3.7 Table and Figures

Table 3.1: The odds ratio for juvenile coho salmon (coho) and Dolly Varden (DV).

Streams	SFC		WPC		IVS		BBS		RPC	
	coho	DV	coho	DV	coho	DV	coho	DV	coho	DV
Juvenile	-1.43	-1.41	-0.76	-0.76	0.31	0.23	-1.33	-1.41	-0.56	-0.55
Chironomidae larvae	3.17	2.57	2.73	3.07	0.00	0.00	2.78	1.37	1.45	0.63
Chironomidae pupa	1.50	1.65	0.77	1.07	0.00	0.00	0.36	0.12	0.13	0.00
Simuliidae larvae	0.00	0.00	1.60	1.79	0.00	0.00	0.00	0.00	0.00	0.00
Simuliidae pupa	0.90	0.48	0.71	0.11	0.00	0.00	0.00	0.00	0.00	0.00
Ceratopogonidae larvae	0.00	0.00	0.00	0.00	0.79	0.07	0.13	0.34	0.21	0.21
Empididae larvae	0.54	1.17	1.35	1.90	0.03	0.03	0.48	0.36	0.51	0.53
Ephemeroptera	0.17	0.67	0.96	1.25	0.00	0.00	0.48	0.15	0.44	0.50
Plecoptera	0.20	0.10	0.19	0.17	0.65	2.36	0.00	0.00	0.57	1.21
Trichoptera	2.12	0.71	0.93	0.00	0.00	0.00	2.98	0.87	2.75	0.78
Hydracarina	0.39	0.08	0.09	0.16	0.00	0.00	0.00	0.00	0.00	0.00
Cladocera	0.06	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Copepoda										

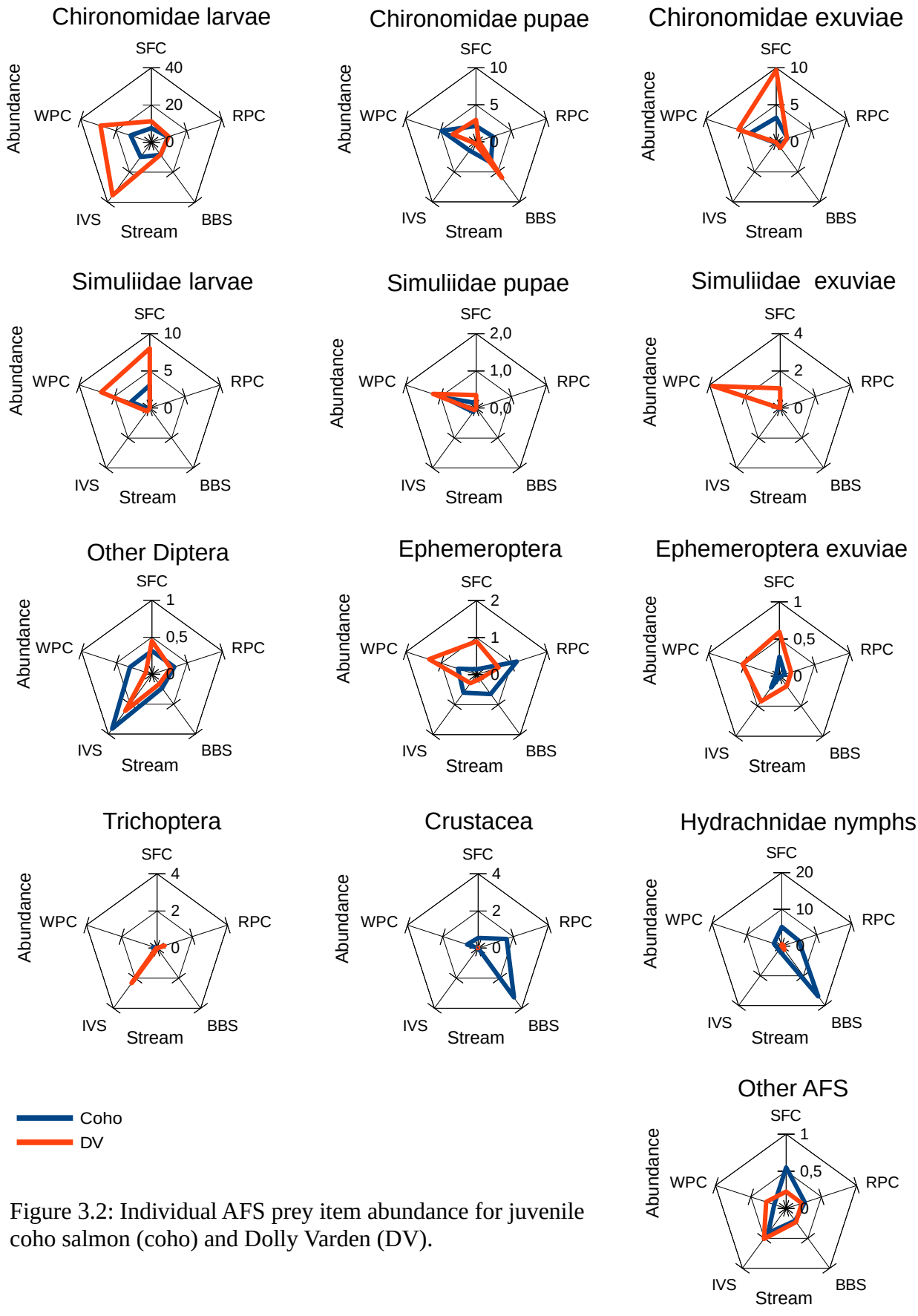


Figure 3.2: Individual AFS prey item abundance for juvenile coho salmon (coho) and Dolly Varden (DV).

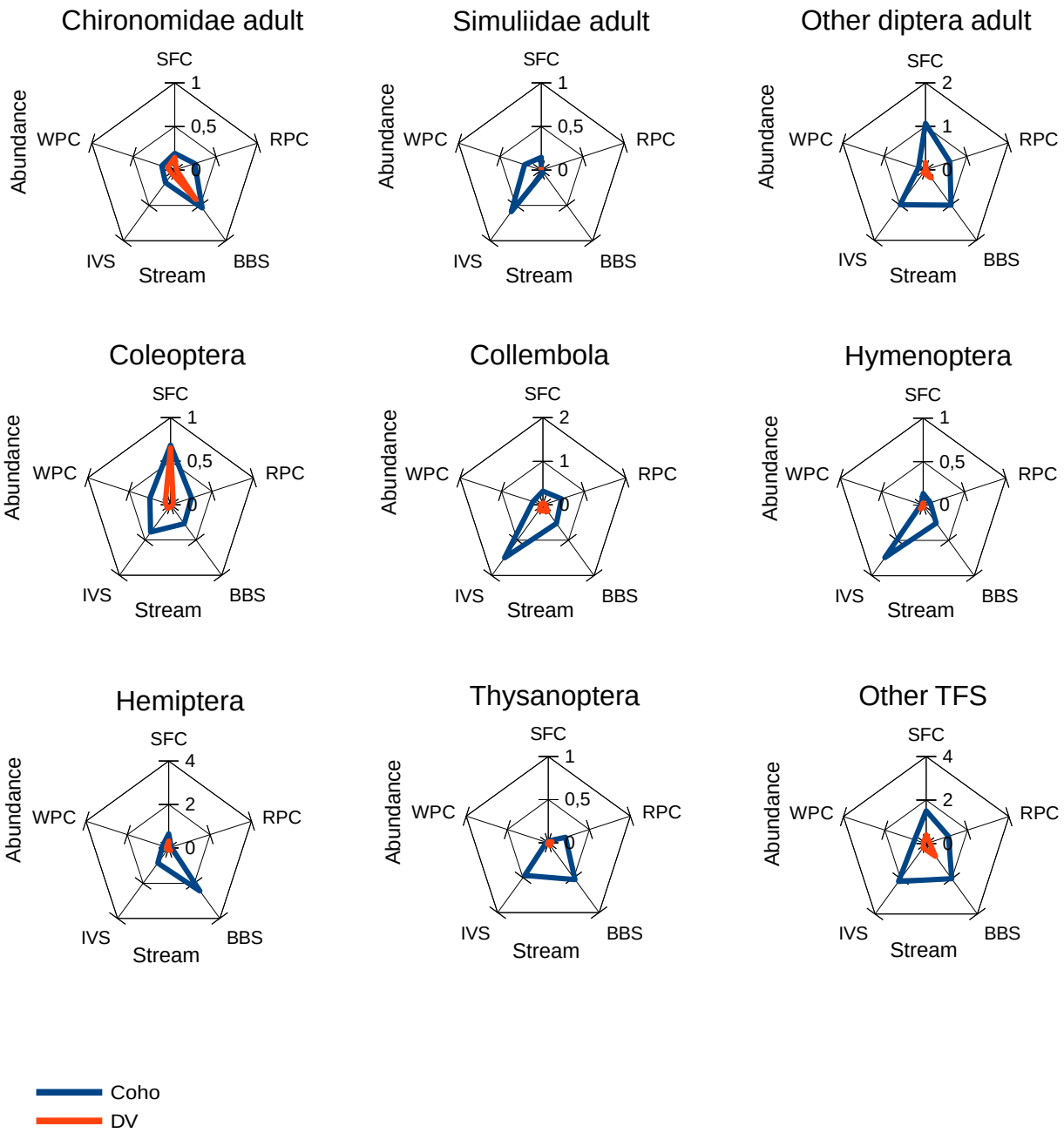


Figure 3.3: Individual TFS prey item abundance for juvenile coho salmon (coho) and Dolly Varden (DV).

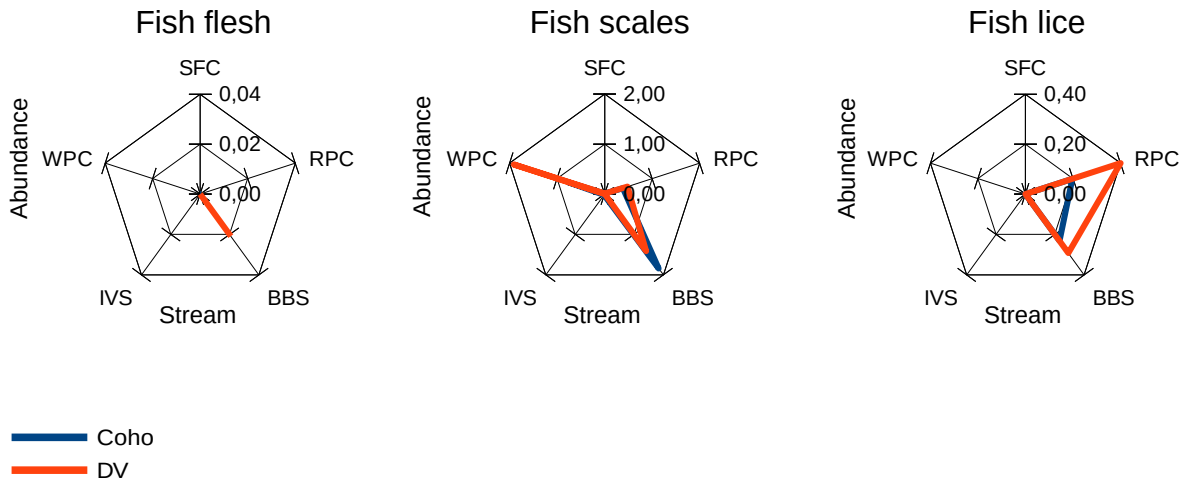


Figure 3.4: Individual MFS prey item abundance for juvenile coho salmon (coho) and Dolly Varden (DV).

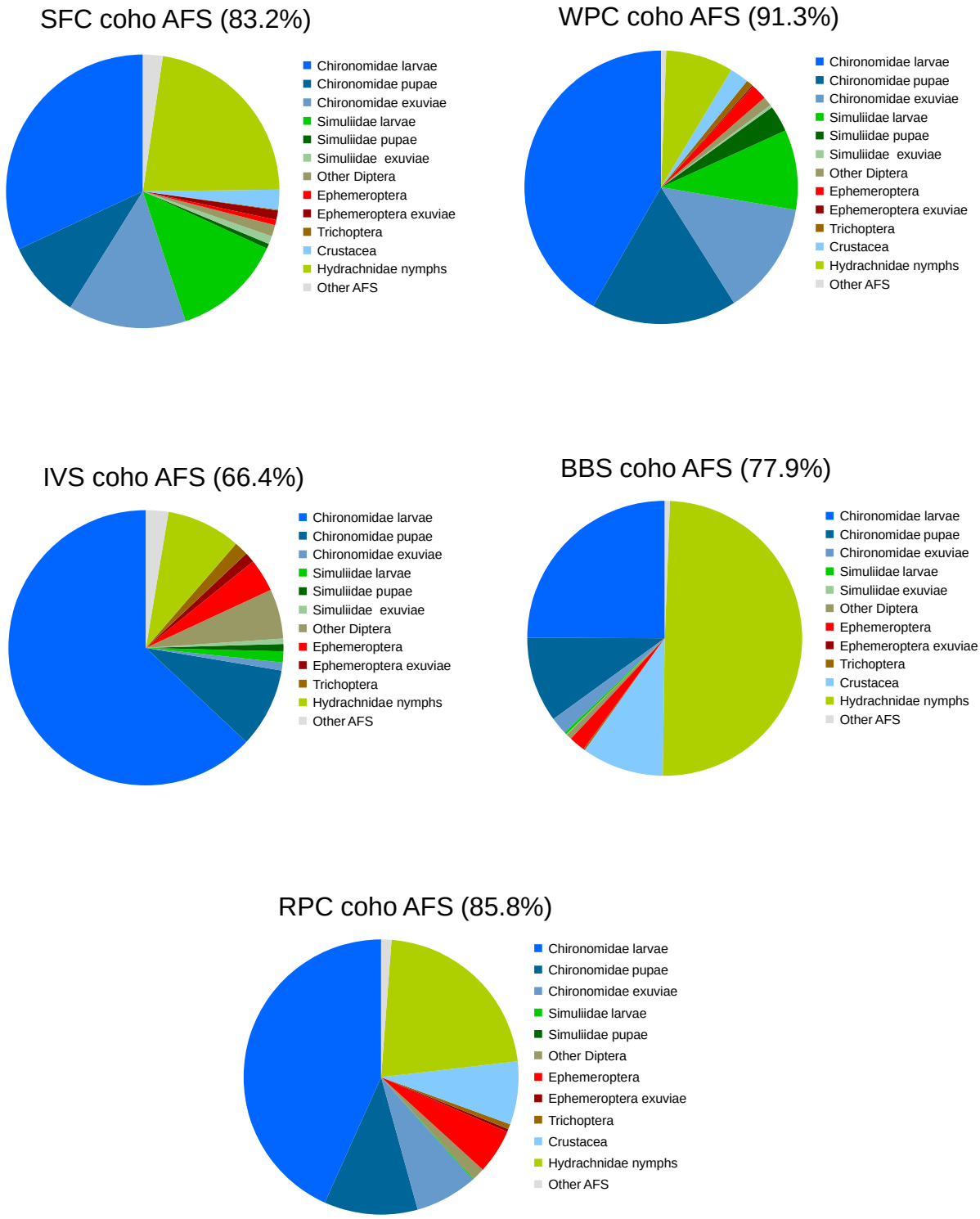


Figure 3.5 a): Percent AFS abundance in the diet for juvenile coho salmon (coho) for all streams.

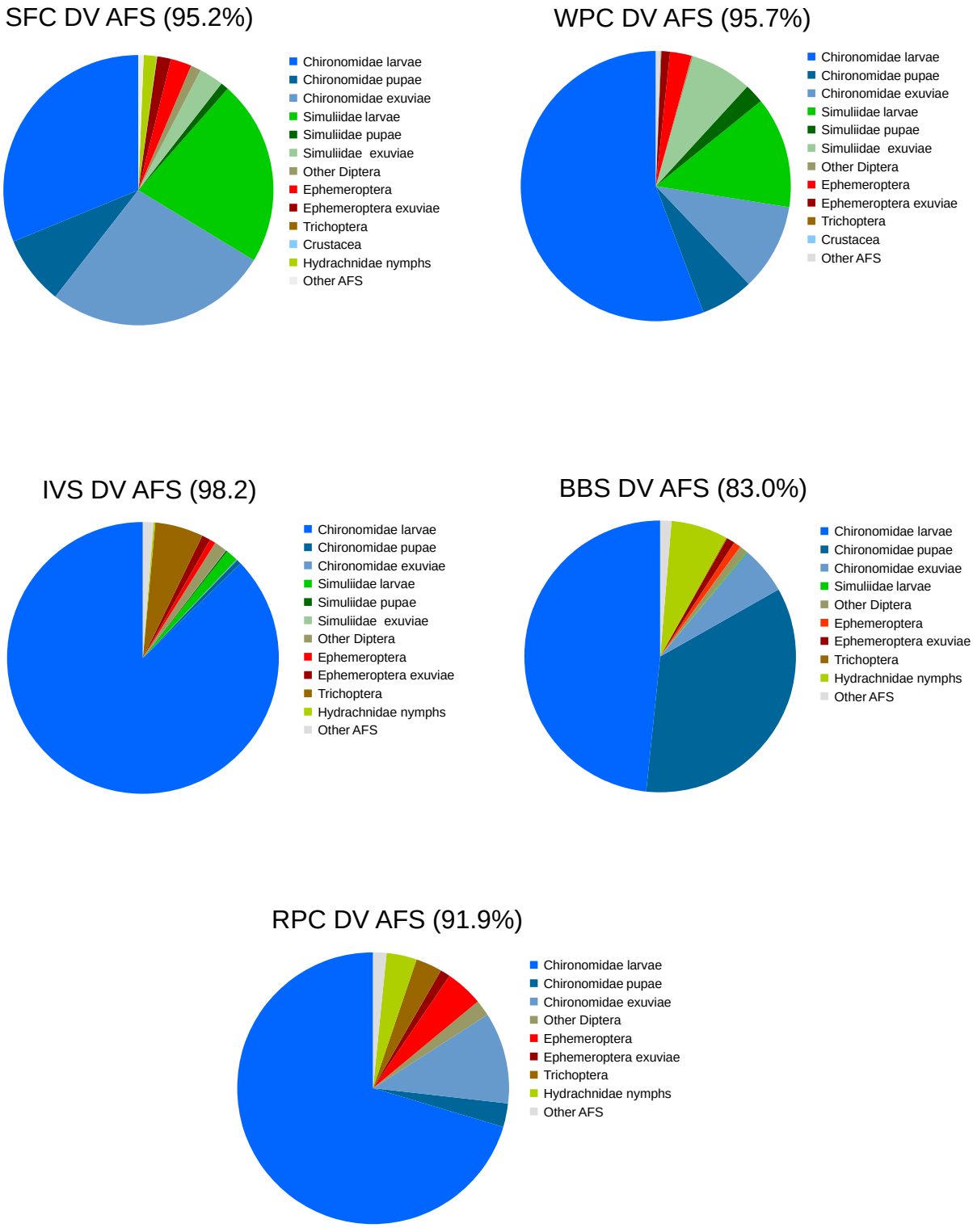


Figure 3.5 b): Percent AFS abundance in the diet for juvenile Dolly Varden (DV) for all streams.

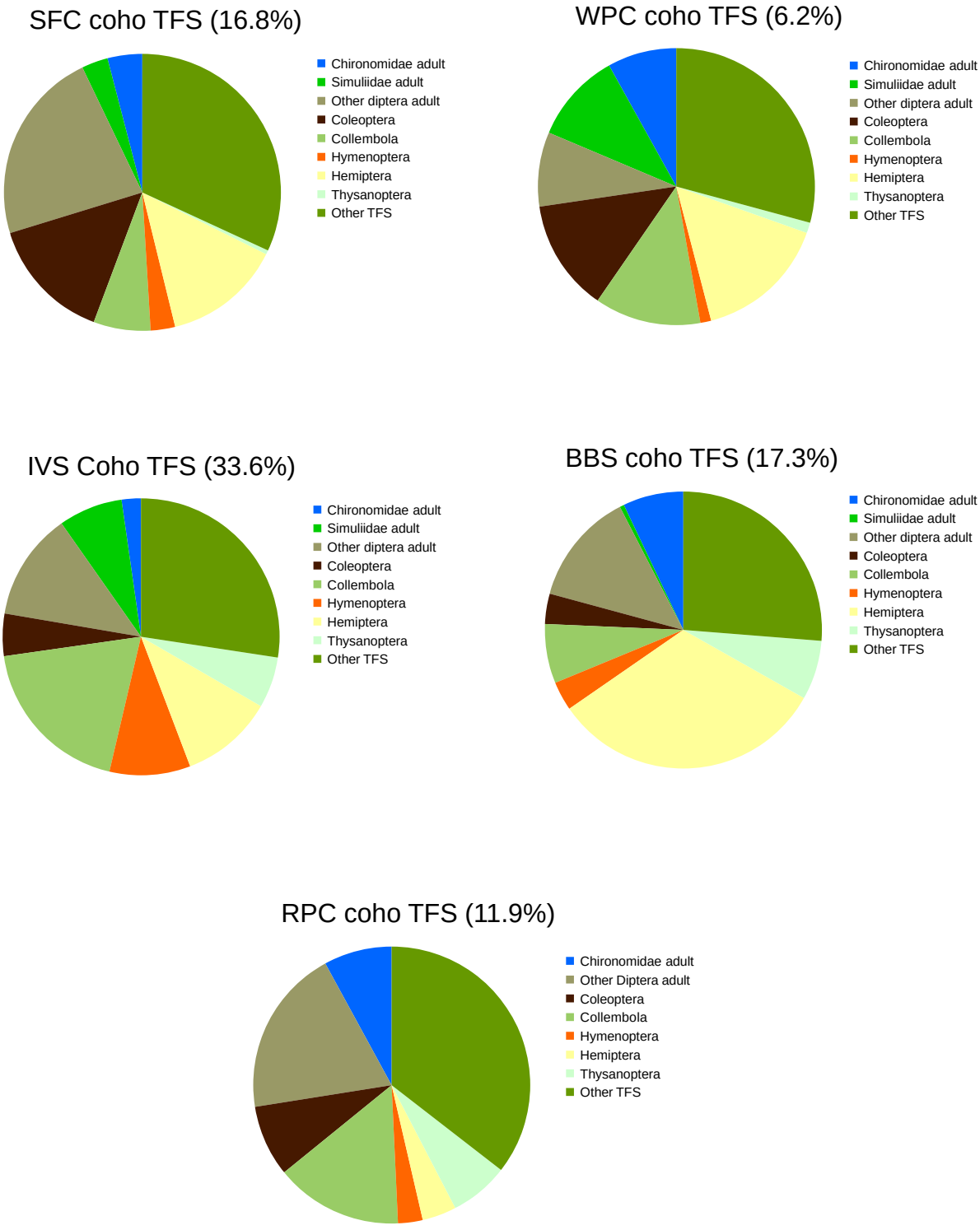


Figure 3.6 a): Percent TFS abundance in the diet of juvenile coho salmon (coho) for all streams.

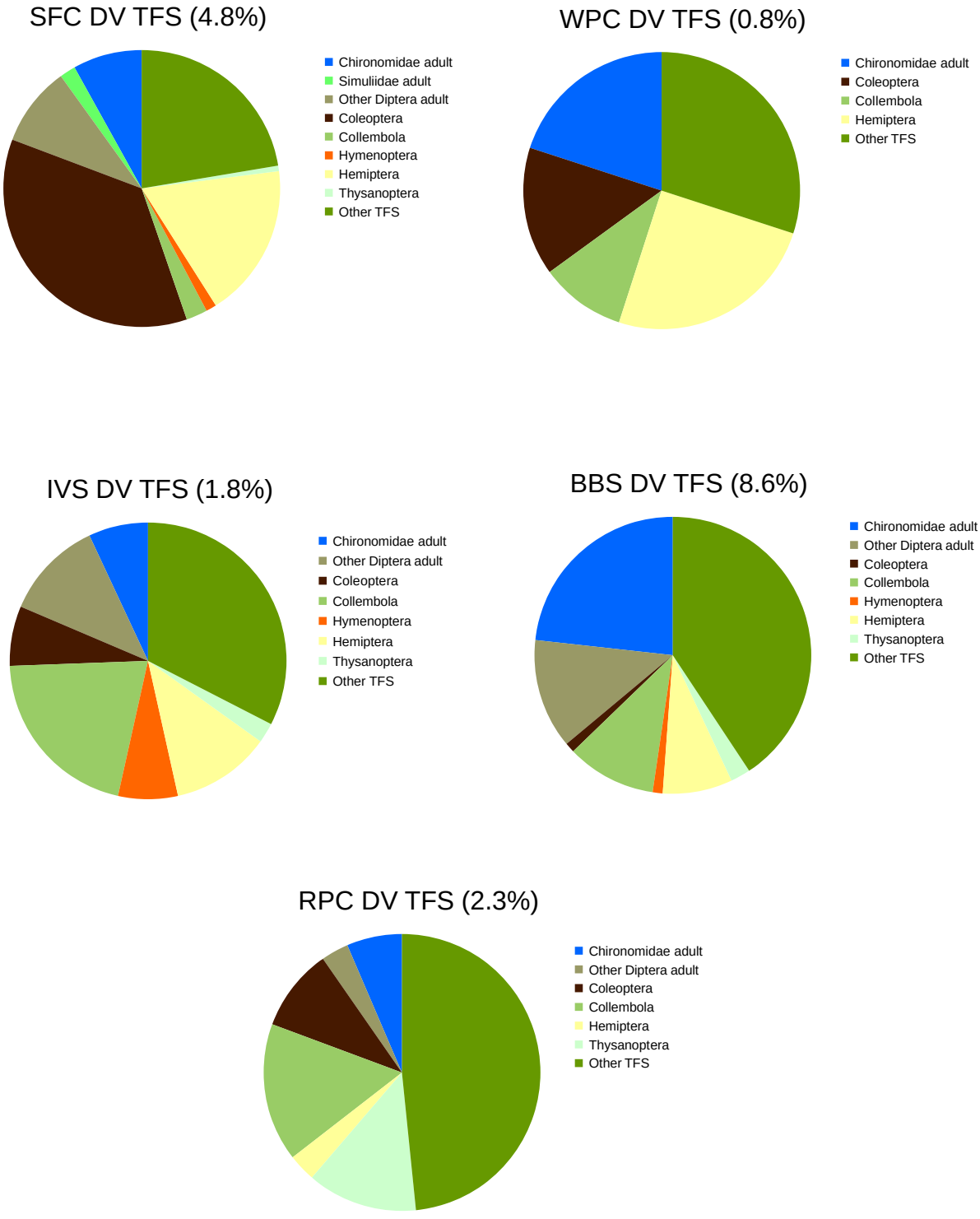


Figure 3.6 b): Percent TFS abundance in the diet of juvenile Dolly Varden (DV) for all streams.

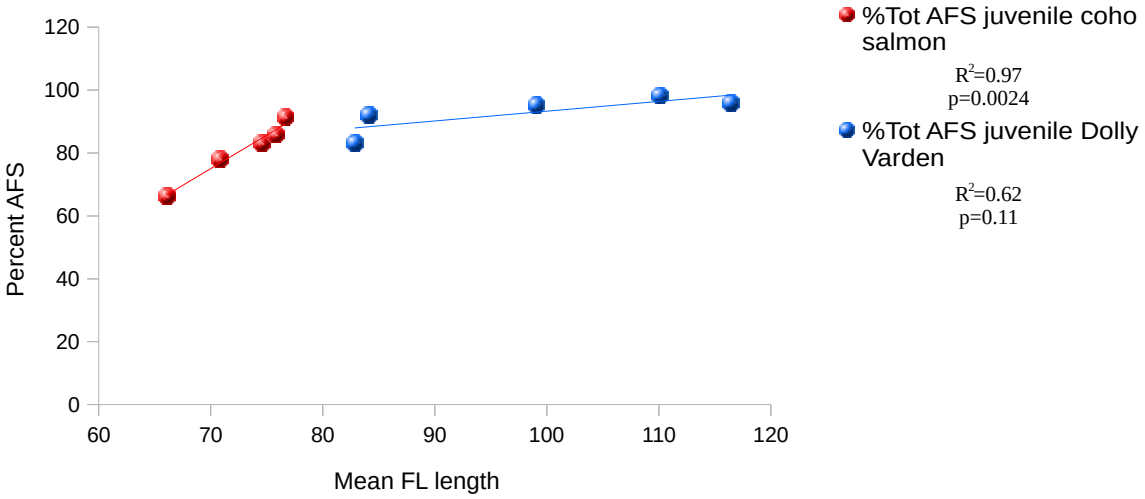


Figure 3.7: Percent AFS items and mean FL per stream.

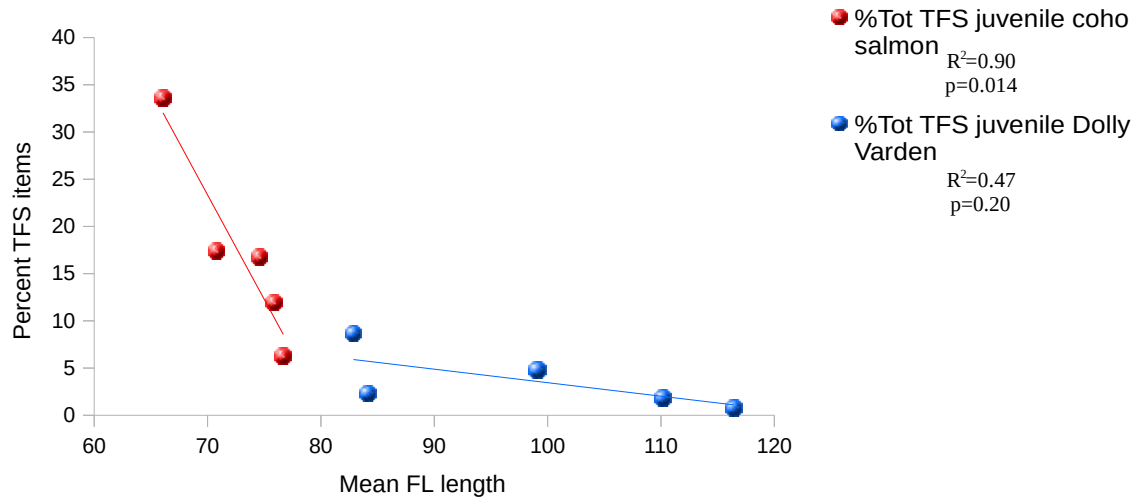
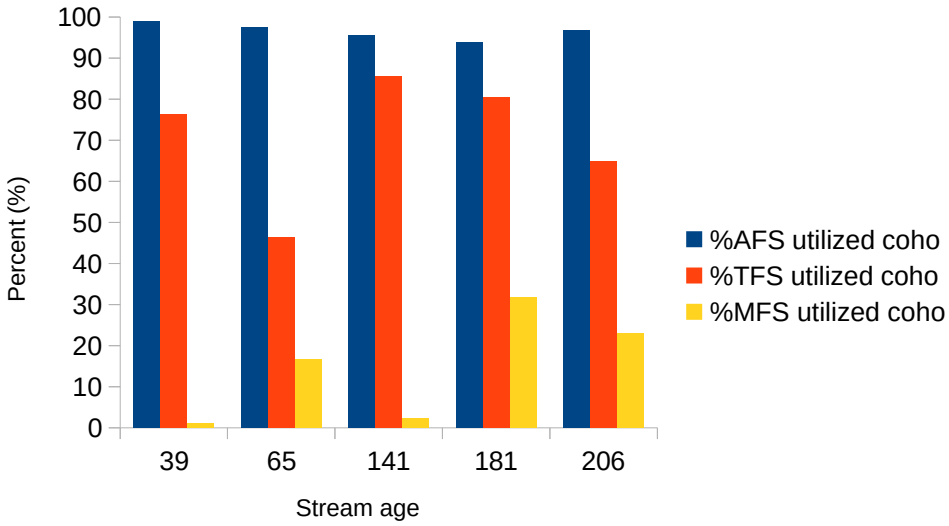


Figure 3.8: Percent TFS items and mean FL per stream.

a)



b)

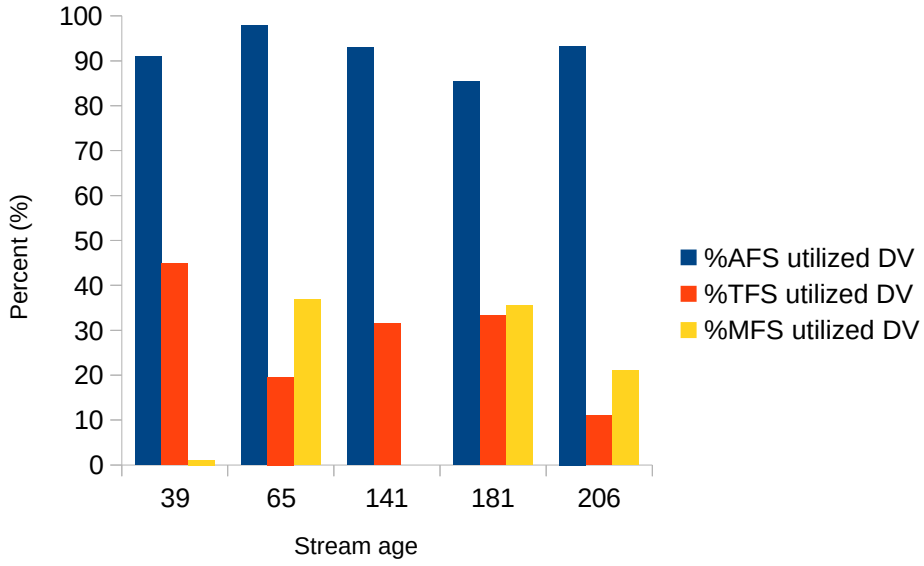


Figure 3.9 a) and b): Juvenile coho salmon (coho) and Dolly Varden (DV) food source utilization per stream.

Table 3.2: Percent AFS, TFS, MFS items by juvenile salmonids and niche breadth and overlap per stream.

		Streams				
Variables	**PCA**	**SFC**	**WPC**	**IVS**	**BBS**	**RPC**
Age	a	39	65	141	181	206
Mean FL juvenile coho salmon	b	74,57	76,68	66,07	70,78	75,84
Mean FL juvenile Dolly Varden	c	99,10	116,41	110,12	82,88	84,13
Niche breadth juvenile coho salmon	d	0,54	0,41	0,57	0,52	0,44
Niche breadth juvenile Dolly Varden	e	0,43	0,31	0,35	0,39	0,24
Morisitas ovelap index	f	0,81	0,91	0,77	0,56	0,82
%AFS per juvenile coho salmon	g	0,81	0,90	0,67	0,67	0,81
%TFS per juvenile coho salmon	h	0,19	0,06	0,31	0,21	0,14
%MFS per juvenile coho salmon	i	0,00	0,02	0,00	0,08	0,03
%AFS per juvenile Dolly Varden	j	0,83	0,89	0,85	0,66	0,85
%TFS per juvenile Dolly Varden	k	0,07	0,02	0,08	0,08	0,02
%MFS per juvenile Dolly Varden	l	0,00	0,07	0,00	0,12	0,06
%Empty gut juvenile coho salmon	m	0,00	0,02	0,02	0,04	0,02
%Empty gut juvenile Dolly Varden	n	0,09	0,02	0,07	0,15	0,07

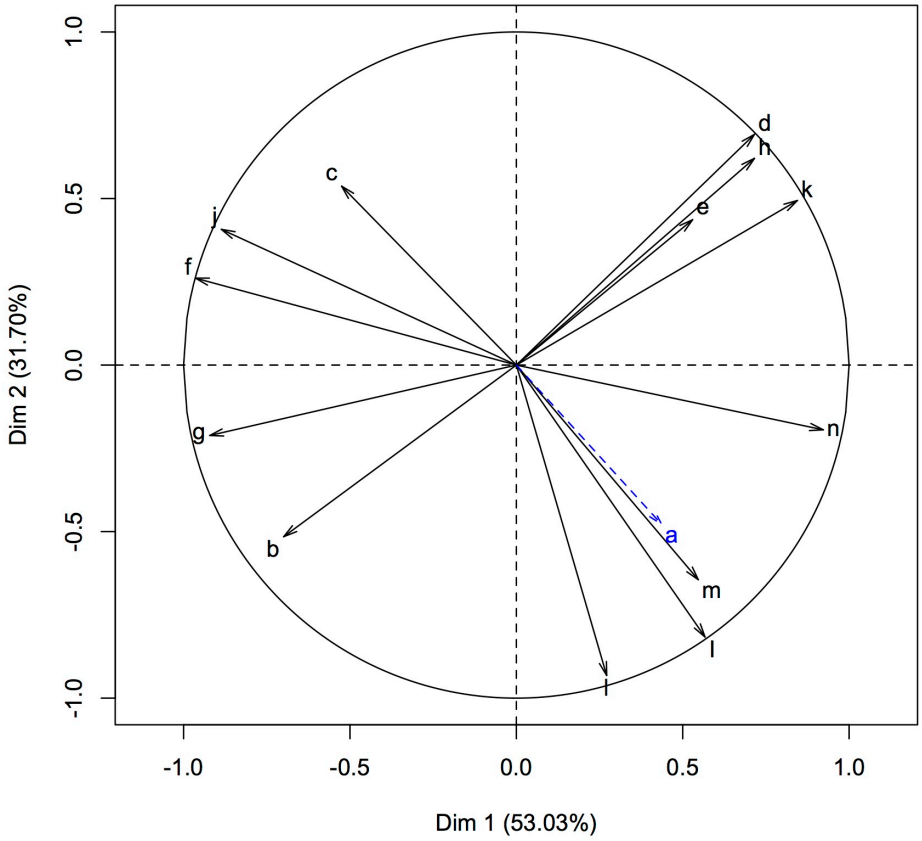


Figure 3.10: PCA of the above factors.

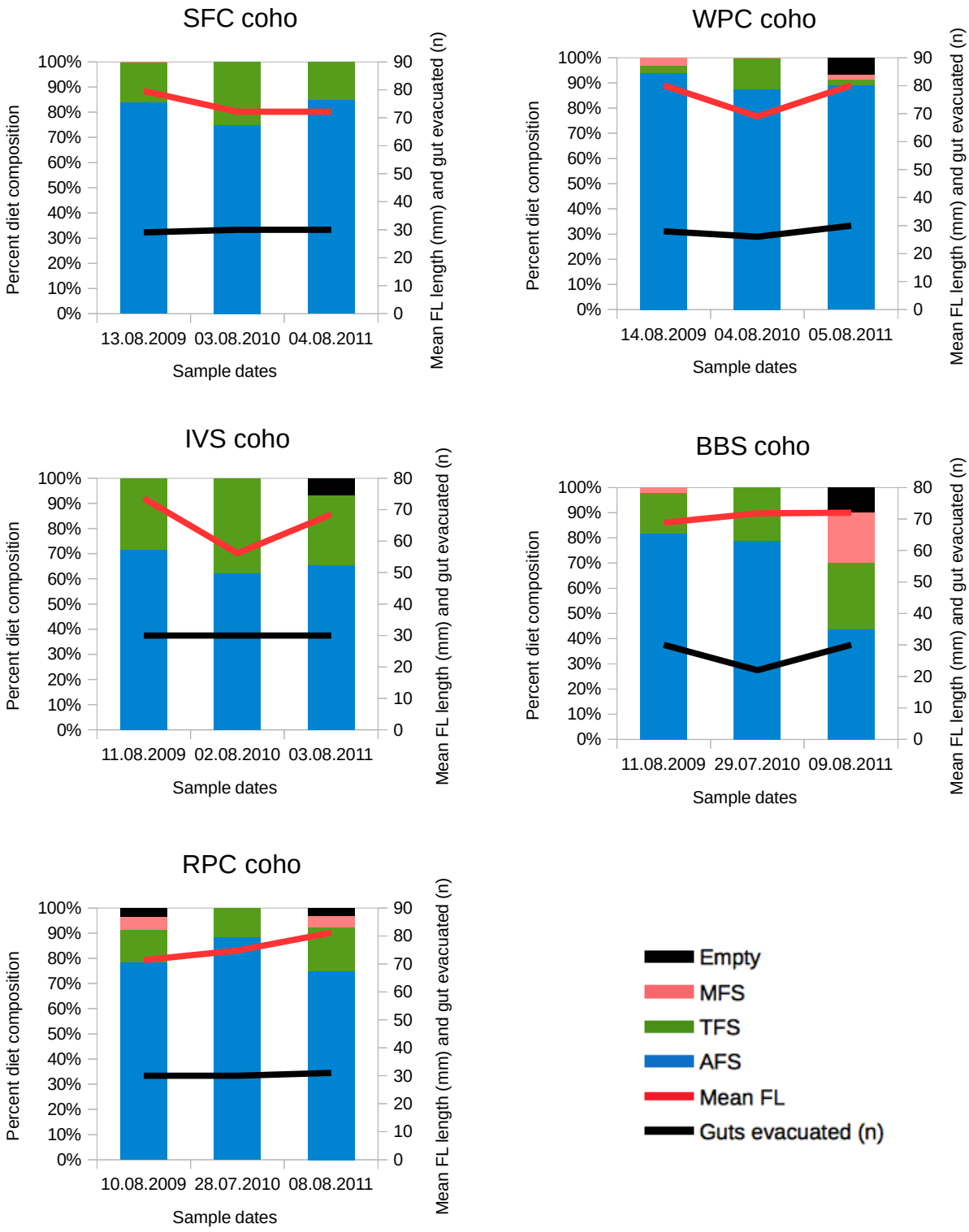


Figure 3.11 a): percent AFS, TFS, MFS and empty gut per sampling time, n fish evacuated and mean FL for juvenile coho salmon (coho).

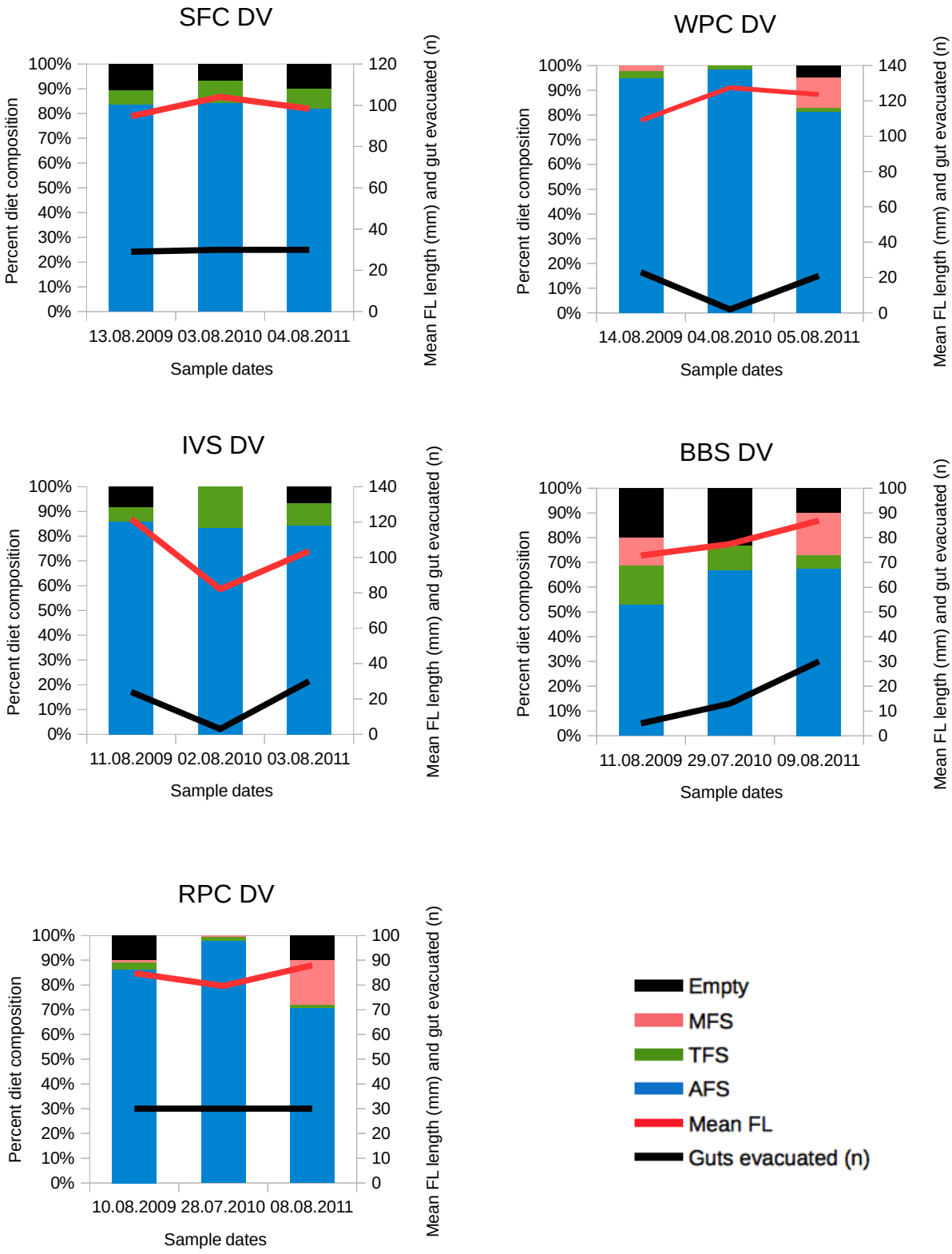


Figure 3.11 b): percent AFS, TFS, MFS and empty gut per sampling time, n fish evacuated and mean FL for juvenile Dolly Varden (DV).

4: Influence of marine derived nutrients in streams of different age and complexity.

Abstract

Pacific salmonids transport marine derived nutrients (MDN) to their natal streams following migration to spawning habitats. This MDN potentially increases stream productivity with respect to macroinvertebrates and juvenile salmonids, and to the proximal environment food webs. Isotopic $\delta^{15}N$ and $\delta^{13}C$ of stream biota were measured to provide insights of MDN levels in five streams of different age (39 to 206 years) since the uncovering of the stream mouth by glacial retreat in Glacier Bay, Alaska. Spawner abundance estimates of pink salmon (*Oncorhynchus gorbuscha*) were undertaken in August 2009-2011. Mean catch per unit effort (CPUE) and mean fork length (FL) were determined for juvenile coho salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*) during 2009-2011 to assess their response to MDN contribution by pink salmon. MDN contribution to stream biota was found to be influenced by pink salmon spawner abundance and retention with stream age, and the effect of MDN is observed to diminish from aquatic to semi-aquatic to terrestrial. Glacier Bay physical habitat development after deglaciation with age shows MDN dispersion (SD) increase and will mask some of the effect of MDN contribution. $\delta^{15}N$ and $\delta^{13}C$ range follow amount of MDN, and caution should therefore be used when analyzing food web size or niche breadth with stable isotopes alone, since $\delta^{15}N$ and $\delta^{13}C$ range decrease the mean $\delta^{15}N$ and $\delta^{13}C$ increase. While MDN was not found to significantly influence abundance of juvenile coho salmon and Dolly Varden, mean $\delta^{13}C$ and the mean FL juvenile Dolly Varden showed a relationship in PCA space, indicative of MDN influence on juvenile Dolly Varden growth. On the other hand, the range of %C and %N seems more important in determining both CPUE and FL for juvenile coho salmon. Future research needs to consider the watershed physical habitat influence on isotopic $\delta^{15}N$ and $\delta^{13}C$ dispersion and range when comparing salmon

populations and their contribution of MDN to different streams, and when analyzing food webs or trophic niche breadth.

4.1 Introduction

Sequestered MDN during the ocean phase of Pacific salmon is transferred to their natal stream when they return to spawn. The ecological effect of Pacific salmonids as a positive feedback on the natal watersheds has been debated (Rex et al. 2014). Multiple trophic levels incorporate MDN, which demonstrate the ecological significance of anadromous annual return in sustaining freshwater food web productivity (Chaloner and Wipfli 2002). Hicks et al. (2005) found juvenile coho salmon obtained 10-50% of their dietary N and C through direct consumption of eggs and carcass material. Wipfli et al. (2003) observed that their fork length increased and Bilby et al. (1998) observed an increase in fish condition factor where salmonid carcasses were added. Measurements of MDN in 2004 in Stonefly Creek (SFC) and Wolf Point Creek (WPC) indicated salmon carcasses as an important nutrient source.

MDN are considered to have a major influence on stream and riparian terrestrial communities (Levy 1997). Nutrient subsidy by MDN has been found to significantly enhance growth rates of Sitka spruce near spawning streams (Helfield and Naiman 2001), and isotopic analysis indicates that trees and shrubs near spawning streams derive approximately 22-24% (24-26% (Helfield and Naiman 2002) of their foliar nitrogen from MDN. While Gende and Quinn (2006) found, in some cases, 70% of foliage nitrogen in trees and shrubs stream side to originate from salmon MDN. Riparian forests again affect in-stream habitats through sediment and nutrient filtration, and the input of coarse woody debris (CWD), which again not only enhance riparian production and act as a positive feedback mechanism for salmon spawning and rearing habitat (Helfield and Naiman 2001), but also enhances the streams

capability to retain more salmon carcasses. Cederholm and Peterson (1985) observed a general positive trend of carcasses being retained by debris in the stream channel ($r = 0.61$).

Kling (2000) highlighted the uniqueness of Glacier Bay as a natural laboratory, to evaluate aquatic ecosystem response to the interaction of landscape geomorphology, climate change and biotic variables. The chronosequence in Glacier Bay provides a range of different stream conditions and a habitat suitability for salmon colonization (Milner et al. 2000). This again provides a unique opportunity to assess MDN variation in watersheds of different complexity over time within the area affected by the Little Ice Age, LIA. The youngest stream, SFC, in our study was colonized within 10 years of stream formation by pink salmon and Dolly Varden char, and thereafter followed by other fish species, among them sockeye salmon (*Oncorhynchus nerka*), coho salmon and coastrange sculpin (*Cottus aleutic*us) and sticklebacks (*Gasterosteus aculeatus*) (Milner et al. 2011). Milner et al. (2000) found indications that colonization and succession were significantly related to stream age, and that fish abundance and diversity may depend on stream habitat complexity and stability. The rapid colonization of salmonids shows the interconnectedness of marine-, freshwater- and terrestrial ecosystems, and will rapidly make MDN available to these new systems.

The amount of MDN delivered to the stream systems is influenced by the abundance of spawning salmonids, but the mechanism of nutrient delivery is not well known (Rex and Petticrew 2008, 2010). Microbial autotrophs and heterotrophs assimilate compounds containing nitrogen and phosphorus excreted from live salmon during salmon runs (Tiegs et al. 2011). Heintz et al. (2004) demonstrated an immediate nutritional benefit from salmon carcass introduction to juvenile coho salmon, and found lipid increase with salmon carcass introduction. MDN from previous spawning events could also indirectly have a strong positive time-delayed impact on the productivity of salmon streams (Nelson and Reynolds 2014), as Bilby et al. (1996) found the highest MDN enrichment of stream biota the following spring.

Cross-environment MDN transport can be significant, as observed from both nesting seabirds (Harding et al. 2004, Maron et al. 2006) and migrations of anadromous spawning fish (Levy 1997, Cederholm et al. 1999, Chaloner and Wipfli 2002, Hicks et al. 2005, Tiegs et al. 2011). For a long time scientists have observed the role of carcasses in providing food for terrestrial consumers (Cederholm et al. 1999). Salmon utilization by bears, wolfs, gulls and other mammals contribute to dispersal of MDN further into the watersheds. Cross-boundary MDN could enhance nutrient poor recipient systems (Nelson and Reynolds 2014), and different salmon species may contribute varying amounts of MDN due to differences in spawning densities and biomasses (Cederholm et al. 1999). Fifty species of terrestrial vertebrates have been identified to utilize salmon carcasses as a food source in Washington (Gende and Quinn 2006). They would all help transport MDN further into terrestrial environments, and white spruce (*Picea glauca*) foliar $\delta^{15}N$ was inversely proportional to the distance from salmon spawning streams (Hilderbrand et al. 1999). Darimont and Reimchen (2002) detected a seasonal shift in the diet of gray wolf (*Canis lupus*), indicating MDN contribution from salmon runs.

Use of stable isotopes is rapidly increasing to analyzing biogeochemical problems in ecosystems, as they can contribute to source-sink and process information (Peterson and Fry 1987). The combination of source and processes of natural distributed $\delta^{15}N$ and $\delta^{13}C$ give an indication of C and N flow through ecosystems (Peterson and Fry 1987). Natural occurring ratios of $\delta^{15}N$ and $\delta^{13}C$ in animal tissues are a combination of source material and specific fraction processes in the different tissues (Dalerum and Angerbjörn 2005). Discrimination of $\delta^{15}N$ and $\delta^{13}C$ is known to vary according to species, tissue, age, growth rates and food quality (Caut et al. 2008), making it difficult to estimate their effect; these authors demonstrated a decrease in discrimination of $\delta^{15}N$ and $\delta^{13}C$ for all tissues with an increase in $\delta^{15}N$ and $\delta^{13}C$. Fish and birds that feed both in freshwater and marine environments during

their life cycle are intermediate between animals feeding exclusively in one or the other environment systems (Schoeninger and DeNiro 1984).

Whole body $\delta^{15}N$ values are usually more positive than those of their diets (Deniro and Epstein 1981). Schoeninger and DeNiro (1984) found on average a 3‰ difference in $\delta^{15}N$ values of animal bone collagen between successive trophic level in terrestrial and marine environments. There is a greater variation in $\delta^{15}N$ values between species on the same diet, compared to same species on different diet, and individuals raised on the same diet can have significantly different $\delta^{15}N$ values (Deniro and Epstein 1981). $\delta^{15}N$ values in bone collagen from animals exclusively feeding in marine environments were on average 9‰ more positive than animals exclusively feeding in the terrestrial environment (Schoeninger and DeNiro 1984).

DeNiro and Epstein (1978) found that the whole body of an animal is, on average, enriched in $\delta^{13}C$ by about 1‰ relative to the diet. The enrichment varies depending on species, their diet, availability and their uptake of $\delta^{13}C$. Large differences in $\delta^{13}C$ are mostly seen if plant and plankton is possessing either C3 or C4 pathway and are easy distinguishable (Peterson and Fry 1987). France and Peters (1997) found the average trophic fraction of $\delta^{13}C$ to increase from + 0.2‰ in freshwater to 0.5‰ in estuarine to +0.8‰ for coastal and + 1.1‰ in open-ocean food webs.

The objectives of this study were to determine if i) MDN is linked to the number of pink salmon spawners, ii) contribution of MDN increases with stream age and watershed complexity, and iii) whether MDN contribution influences instream juvenile salmonid growth and abundance. Three hypotheses were proposed: 1. Pink salmon spawner abundance controls the contribution of MDN. 2. MDN will show an increase with stream age and steam complexity. 3. MDN will influence the abundance and growth of juvenile salmonids.

4.2 Methods

4.2.1 Study streams

The study streams were located in Glacier Bay National Park in southeast Alaska; an area encompassing a fjord with two major arms that has experienced glacial retreat since around the mid 1700. Chapin et al. (1994) documented four major successional stages of terrestrial vegetation in Glacier Bay. Five streams aged from 39 years to 206 years, Stonefly Creek (SFC), Wolf Point Creek (WPC), Ice Valley Stream (IVS), Berg Bay South Stream (BBS), and Rush Point Creek, (RPC) (Figure 4.1). Stream age determination of Stonefly Creek was as described in Milner et al. (2000), where stream age is defined as the time since the start of the ice recession from stream mouth by use of historical, satellite and aerial photographs, journal articles and unpublished data. To make these findings more comparable stream sites selected were long time sample sites (Milner, Sønderland).

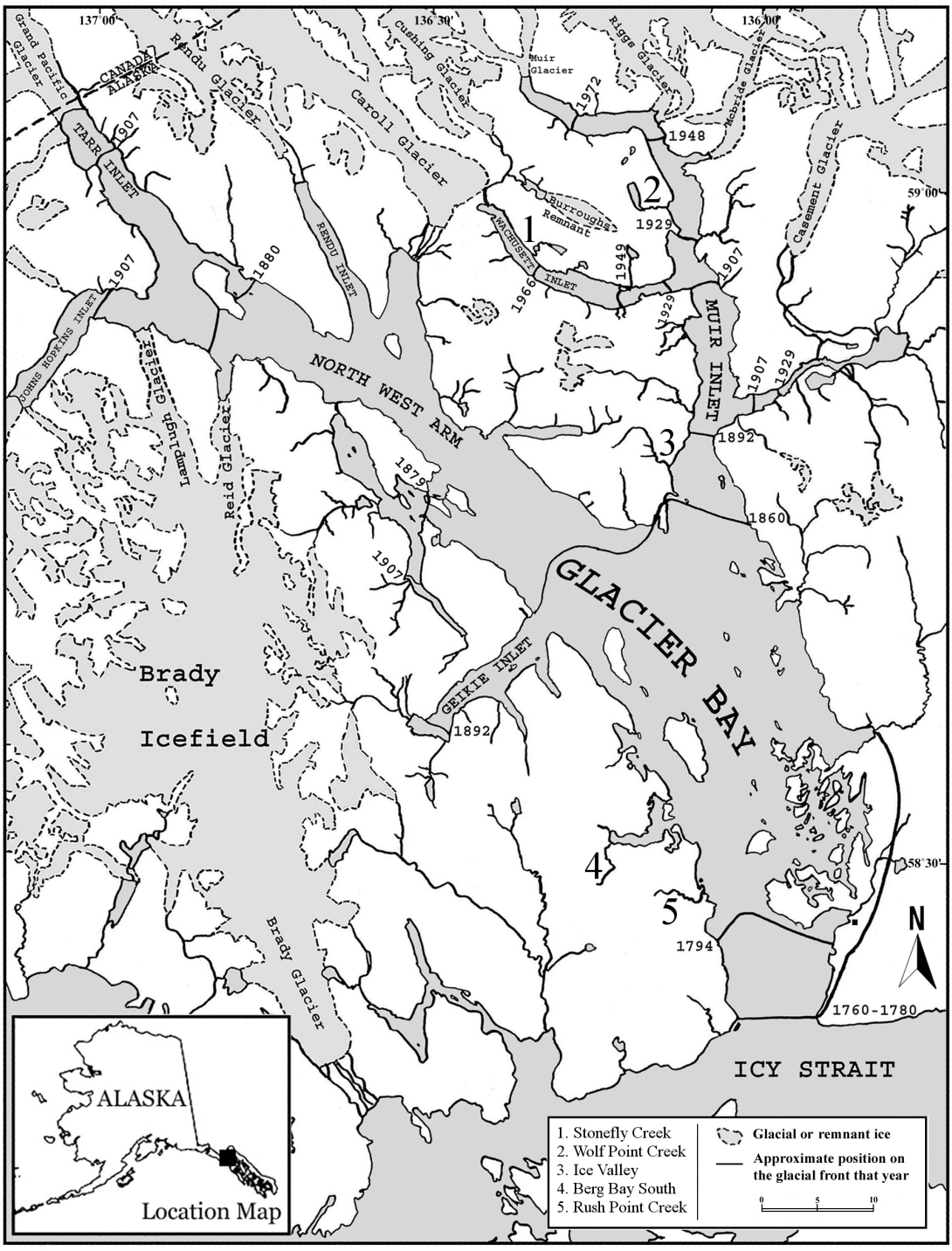


Figure 4.1: Location of the five study streams.

4.2.2 Biota collection and analysis

Common prey groups were selected based on gut evacuation of juvenile coho salmon from 2009. Collected samples were divided into the three environments of capture; terrestrial, semi-aquatic and aquatic to see the effect of different environments in and proximal to the stream. Willow, aphids and adult Simuliidae were classed as terrestrial, moss and wolf spiders were classed as semi-aquatic and biofilm, larval Simuliidae and Chironomidae, juvenile coho salmon and Dolly Varden were classed as aquatic.

Juvenile fish were captured in 2011 by minnow traps (400mm x 220mm, with a 6mm mesh) baited with salmon eggs soaked in iodine (enclosed inside "Kinder Eggs" capsules with small holes) to ensure that the juvenile salmonids not could consume any eggs. Traps were fished for 1.5h, and 54 juvenile salmon were retained for stable isotope analysis (two to five fish of 0+ and 1+ juvenile coho salmon and Dolly Varden). A small piece of muscle tissue was removed between the head and the adipose fin of juveniles and placed into Eppendorf tubes or plastic vials for the 1+ and larger juveniles. Biofilm was collected by brushing stream rocks in a tray of water, followed by filtration for sample accumulation and placed into Whirl-Pack bags. New foliage (approx. five) from riparian willows were collected and stored in plastic bags. Moss and spiders were collected at the side of the stream (approx. five and one per sample respectively). Aquatic macroinvertebrates were collected from kick samples and picked from in-stream substrate (approx. three per sample). Terrestrial invertebrates were collected with sweep nets and aphids were picked from foliage proximal to the stream and placed in Eppendorf tubes (approx. three per sample). All samples were stored on dry ice until placed into a freeze dryer in the lab. After freeze drying (lyophilization), the samples were finely ground up and homogenized with a mortar and pestle and a Wig-L-Bug (Crescent Dental Manufacturing Co).

Isotope ratios of $\delta^{13}C/\ \delta^{12}C$ and $\delta^{15}N/\delta^{14}N$ were determined for two to four samples of each group with a continuous-flow Roboprep /Europa 20/20 system (sample signal < 20mV were rerun with a larger sample). Due to time constraints in the field no evacuation of the macroinvertibrates was performed, nor any respiratory CO_2 removed. All samples were ground whole to more easily comparable samples, except for the fish. Preferably the whole body should have been used (DeNiro and Epstein 1978), however salmonid tissue were used, as this did simplify the sampling process.

No lipid extraction was performed, as this extraction has been shown to skew $\delta^{15}N$ values (Bodin et al. 2007, Mintenbeck et al. 2008, Boecklen et al. 2011, Ryan et al. 2012). Surface lipid extracts $\delta^{13}C$ values of C4 and CAM species have been found on average 8‰ more depleted in $\delta^{13}C$ than the leaf tissue values, while surface lipid extract $\delta^{13}C$ values of C3 species were on average 4‰ more depleted in $\delta^{13}C$ (Collister et al. 1994). Hammer et al. (1998) found Texas redhead ducks had more positive $\delta^{13}C$ values in the fatty acids than those of identical fatty acids in seagrass. Differences in $\delta^{13}C$ in lipids could therefore produce a bias when lipids are extracted when comparing samples across trophic levels, as each different type of lipids may contain different $\delta^{13}C$ values, and vary among species, season and diet. Lipid correction was not performed as the fractionating of each macroinvertebrate is not known, and as different corrections would be needed for the terrestrial samples compared to the aquatic. Lipids could also sometimes have higher $\delta^{13}C$ levels than other fractions or the entire body itself (DeNiro and Epstein 1978), depending on the food source, even though the organisms would most likely be depleted in $\delta^{13}C$, relative to proteins and carbohydrates (Post et al. 2007). The homogeneity when grinding is important to ensure the sample weighed out represents the whole body.

Instead of using a mixing model the dispersion (SD) and range (min to max) of the stable isotopes collected was calculated to understand change with stream age and food web complexity.

4.2.3 pink salmon counts, juvenile salmonid measurements and statistics.

Adult pink salmon spawner count was undertaken in August 2009 to 2011 by averaging the hand-held counters used by two people on opposite sides of the stream. Pink salmon were only counted in the main channel of the study streams, and although other salmonids spawned in these streams, pink salmon spawner abundance was much greater. A three year average was used due to the delayed pulse of MDN (Nelson and Reynolds 2014) and to possibly better account for the retention of MDN within the watersheds, due to difference in even and odd year spawning numbers (Milner and Bailey 1989). A three year mean for catch per unit effort (CPUE) and fork length (FL) for juvenile coho salmon and Dolly Varden were calculated for better adjust for differences between the years, and better link MDN fluxes and retention. Isotopic $\delta^{15}N$ and $\delta^{13}C$ measurements, were only sampled in 2011, and change in MDN by year can not be addressed.

Statistics analysis were performed in R v.3.1.2 (GUI 1.65), where one-way-ANOVA was used to assess the variance of $\delta^{15}N$ and $\delta^{13}C$ between study streams. Principal component analysis (PCA) biplot was then calculated to assess directional relationship between the different streams.

4.3 Results

4.3.1 Marine derived nutrients Isotope analyses

Both mean $\delta^{15}N$ and $\delta^{13}C$ were significantly different between streams (one-way ANNOVA, $P < 0.01$). Mean $\delta^{15}N$ and $\delta^{13}C$ (2011) with mean pink salmon spawner abundance (2009-2011) are found in Figure 4.2. The mean stream $\delta^{15}N$, $\delta^{13}C$, %N and %C, and the dispersal (SD) and Range (min to max value), as well as C/N ratio and FL, CPUE, spawning abundance are found in Table 4.1, and their directional relationship are found in a PCA space (Figure 4.3). Two adult sockeye salmon were sampled from SFC as a reference, showing similar values: $\delta^{15}N$ 10.19‰ and 10.26‰, $\delta^{13}C$ -22.19‰ and -22.29‰.

The lowest value of $\delta^{15}N$ (-4,8‰) was willow found in IVS with a range (-4.805‰ to -3.637‰), and Chironomidae from IVS was the only macroinvertebrate taxa which was lower than -3‰. In IVS also one juvenile 0+ and 1+ coho salmon with a $\delta^{15}N$ value below 4‰, even though one 1+ coho was as high as 8,1‰, ranging (3.615‰ to 5.858‰) and (3.837‰ to 8.079‰) respectively. Overall IVS showed lower $\delta^{15}N$ values than the rest of the streams, with lowest aphid value -2,5‰ and adult Simuliidae value -0,03‰, with a range of (-2.499‰ to -1.294‰) and (-0.30‰ to 1.054‰) respectively. On the other end willow leaves from WPC showed one $\delta^{15}N$ sample at -0.164‰ (range -3.203‰ to -0.164‰). The highest aphid value was found in SFC with -1,25‰, while the highest average was found in WPC -1.3‰. The highest $\delta^{15}N$ value in WFC was not a salmonid but a wolf spider with 7,1‰ (range 5.491‰ to 7.077‰), while 0+ ranging from (4.919‰ to 5.637‰) makes spiders the top predator in WPC. The highest $\delta^{15}N$ value found in our streams was a 0+ coho from BBS with a value as high as 8,2‰ (range 7.568‰ to 8.214‰), with also the highest value of Simuliidae larvae and adults ranging from (3.874‰ to 4.890‰) and (4.963‰ to 5.590‰) respectively.

Chironomidae from RPC was the only taxa that had $\delta^{13}C$ values lower than -39‰, ranging from (-38.943‰ to -39.623‰), while one willow sample from SFC had higher $\delta^{13}C$ values than -28‰, (range -29.224‰ to -27.418‰). The highest recorded $\delta^{13}C$ value in WPC was a 0+ juvenile coho salmon from WPC; -24.140‰, (range -27.199‰ to -24.140‰), while the highest mean was moss from SFC -25.08‰, (range -26.020‰ to 24.426‰).

All streams had a low mean C/N ratio (Figure 4.4), and lowest C/N ratio was found in WPC and BBS, with high pink salmon spawner abundance. Mean %N and $\delta^{15}N$ range in WPC and BBS also confirms the connection to spawner abundance (Figure 4.5). Mean $\delta^{15}N$ diminished from aquatic via semi-aquatic to terrestrial environment, and showed peaks for WPC and BBS (Figure 4.6 a)). Mean $\delta^{13}C$ does not show the same pattern as mean $\delta^{15}N$ except for in WPC (Figure 4.6 b)). The stream biota range of $\delta^{15}N$ and $\delta^{13}C$ decreased with higher mean $\delta^{15}N$ and $\delta^{13}C$ (Figure 4.7 and 4.8), and significantly for $\delta^{13}C$.

Pink salmon and mean $\delta^{15}N$ show similar patterns, while the peak is higher for $\delta^{15}N$ in BBS, where pink salmon spawners abundance is less than WPC, indicates that streams accumulate $\delta^{15}N$ with age (Figure 4.9). Dispersion of samples (SD) of both mean $\delta^{15}N$ and $\delta^{13}C$ increased significantly with stream age. Continuously increase in $\delta^{15}N$ and $\delta^{13}C$ ($R^2 = 0.69$ and $R^2 = 0.99$ respectively), except for mean $\delta^{15}N$ in WPC (Figure 4.10).

The %N and %C range is larger in IVS and BBS, and does not follow salmon spawner abundance (Figure 4.11). The range of %N and %C were found to influence juvenile coho salmon FL and abundance negatively (Figure 4.12 and 4.13).

4.3.2 Salmon spawners and juvenile salmonids.

All streams supported pink, chum (*Oncorhynchus keta*), coho salmon and Dolly Varden. SFC also supports sockeye salmon and juveniles were found in RPC in 2010 for the first time. Pink salmon were used due to their high spawner abundance, and a three year mean of spawner numbers is summarized in Table 4.1. Difference in visibility among the streams made enumeration more difficult. Glacial runoff in SFC and resuspension of glacial fines with high flows in WPC could cause lower enumeration in these streams. WPC supports a much higher abundance of pink spawners compared to the other streams, and has a three year average of 8193 pink salmon whereas the three year average for IVS was 288. Low water level and dry sections of the stream channel were observed in 2009 and 2010 at IVS, and no pink salmon were documented at that time due to low flows low stream water level. Adult pink salmon were however observed in the mouth of the stream waiting for water level to rise and will likely create later run.

4.4 Discussion

4.4.1 MDN contribution by pink salmon spawners

Low mean C/N ratios and high mean $\delta^{15}N$ levels indicates MDN contribution to the stream food web. The lowest C/N ratios and highest $\delta^{15}N$ levels in stream biota were found in the streams with the greatest pink salmon abundance, thereby confirming Hypothesis 1. Watershed environments in Glacier Bay displayed the same across dispersion pattern of mean $\delta^{15}N$, and indicated pink salmon spawners to be controlling MDN contribution from the aquatic to the terrestrial environment. An increase in MDN will decrease the range of $\delta^{15}N$ and $\delta^{13}C$, significantly so for $\delta^{13}C$. This explains why WPC is the only stream where mean $\delta^{13}C$ displayed the same patterns as mean $\delta^{15}N$. Less discrimination of $\delta^{15}N$ and $\delta^{13}C$ (cf Caut et

al. 2008) are therefore a result of higher pink salmon spawner abundance. Differences in spawning densities and biomass between different salmon species (Cederholm et al. 1999) can influence the amount of MDN contribution to the streams, as well as the variation in lifecycle. Typically $\delta^{15}N$ and $\delta^{13}C$ levels in adult pink and sockeye salmon is lower compared to king and coho salmon, while chum salmon are intermediate (Satterfield and Finney 2002). Greater pink salmon spawner abundance in Glacier Bay, compared to other species, indicates that they are the strongest vector for MDN from marine to watershed environments. Sampling later in the fall is needed to confirm this. Stream water level variation affects the timing of upstream migrations, causing yearly variations among spawning salmonids, in addition to the difference between odd and even years of pink salmon spawning abundance (Milner and Bailey 1989). Different utilization of the watershed's stream network by salmonids, migration barriers and watershed retention properties will control how much MDN is stored and available for inhabitants of the watershed. Stream discharge will also affect the retention of carcasses in the stream and high flows could transport carcasses back back into the fjord. Nakayama et al. (2015) found that the outwash of total particulate nitrogen (TPN) to be a function of river discharge. However Alexander et al. (2000) found the loss of nitrogen per unit length decreased with depth and to be approximately three times greater than the decrease in loss per length unit, due to increasing velocity. Many of the streams have smaller and larger barriers for fish migration, which would limit the MDN contribution in the higher reaches. Only Dolly Varden have been observed above the natural barrier found in SFC, and the one Dolly Varden $\delta^{15}N$ value from the upper lake mouth from 2004 was as low as 2,54‰ (earlier findings).

Chaloner and Wipfli (2002) suggested that pathways for MDN included both consumption of salmon material by macroinvertebrates and fish, and uptake of mineralized MDN by biofilm. (Tiegs et al. 2011) observed predictive relationships between live-salmon abundance and stream water nutrient concentrations, and TPN has been observed to strongly correlate with suspended sediment concentrations (Nakayama et al. 2015). This could be due to flocculation, as (Rex and Petticrew 2008) presented a salmon-floc feedback loop, which demonstrated how

salmon re-suspending fine inorganic particulate matter helps the flocculation and subsequent delivery to the stream bed. These authors also highlighted the importance of bacterial extracellular polymeric substance (EPS) in delivering nutrients to the stream bed. Biofilm might be a good way to measure uptake of MDN, as flocculation and retention in the biofilm and sediment will increase the nitrogen levels upwards in the stream food chain (Rex and Petticrew 2008). Tiegs et al. (2011) found that biofilm biomass more closely follows live salmon abundance than the abundance of carcasses. The Simuliidae larvae had however the closest relation to pink salmon spawners, and high $\delta^{15}N$ Simuliidae larvae values in WPC and BBS suggest higher pink salmon spawner densities. Simuliidae larvae is a filter feeder and would more easily absorb any marine fine particulate matter, and may be used as an indicator for MDN, and may also be connected with flocculation of salmonid matter occurring in the streams. The abundance of Simuliidae can be linked to the disturbance caused by salmonid digging spawning redds, thereby facilitating their persistence (Milner et al. 2008). Flooding could also transfer carcasses into the riparian forest (Ben-David et al. 1998), and Koshino et al. (2013) found flooding to transport more salmon carcasses into the riparian area compared to bears did. Chaloner and Wipfli (2002) observed a varied response by macroinvertebrates to salmon-derived input, which could reflect their feeding ecology.

4.4.2 MDN relationship to age and complexity

Age is a response of time and how long the salmon spawners potentially have utilized a stream. Age is closer than pink salmon spawner abundance to mean $\delta^{15}N$ in PCA space and the mismatch of pink salmon and $\delta^{15}N$ with age indicates an accumulation with time, partly confirming Hypothesis 2. This would need to be analyzed further to confirm, preferably by sampling over several years to be able to account for the accumulation of MDN with stream complexity. Juvenile populations also influence the MDN loss when migrating out and make this question very complex in regard to MDN accumulation with age. Large riparian vegetation in the older streams creates an increased input of CWD and an increased size of

CWD, which again provides greater habitat diversity (riffles, runs and pools), enhancing juvenile coho salmon abundance (Milner et al. 2000). Although WPC supported CWD, this was mostly alder and some smaller cottonwood, which do not form such complex structures as spruce and larger cottonwoods. BBS and RPC are the oldest streams, with larger CWD accumulations due to spruce and large cottonwood, which aids retaining MDN and potentially contributes to higher $\delta^{15}N$ levels. Large woody debris (LWD) creates pools and affects channel width and depth (Bilby and Bisson 1998), and directly retains salmon carcasses (Strobel et al. 2009). A second effect of CWD on MDN retention would be creation of pools (Milner and Gloyne-Phillips 2005) increasing MDN retention (Alexander et al. 2000), and is more prevalent in older streams. The dispersion increases for both $\delta^{15}N$ and $\delta^{13}C$ with stream age, except for $\delta^{15}N$ in WPC. Range and dispersion of both $\delta^{15}N$ and $\delta^{13}C$ is likely due to the increase in carbon and nitrogen from other (terrestrial) sources, giving a larger variation in $\delta^{15}N$ and $\delta^{13}C$ uptake due to different utilization of food sources and higher discrimination (Caut et al. 2008). Vegetational succession changes with age and significantly increases the percentage of instream wood and pool habitats, however not significantly affecting channel stability (Milner et al. 2000). The decrease in mean $\delta^{13}C$ in the aquatic, semi-aquatic and terrestrial environment with stream age could be explained by the increased terrestrial input, and a result of vegetation and soil succession (Engstrom et al. 2000). There is a large increase in organic carbon throughout the chronosequence in Glacier Bay (Crocker and Major 1955), leading to an increase in dissolved organic carbon (DOC) in lakes with age (Engstrom et al. 2000, Williamson et al. 2001). During photosynthetic CO_2 fixation there is a preferential utilization of $\delta^{12}C$ and a discrimination of $\delta^{13}C$ (Park and Epstein 1961). Increased carbon input from the terrestrial area in the watershed lead to an increased discrimination against $\delta^{13}C$ (Caut et al. 2008). SFC and WPC also encompass large lakes, and previous work has shown freshwater macrophytes from lake littoral zones to be more enriched in $\delta^{13}C$ compared to the same species collected in fast moving rivers (France 1995). While this could help explain the higher $\delta^{13}C$ levels, WPC also supports the greatest abundance of pink salmon spawners compared to the other streams, and will more likely account for the peak in mean $\delta^{15}N$ and $\delta^{13}C$. The

higher levels of $\delta^{13}C$ in SFC could also be linked to the reason that SFC has sockeye salmon runs, and is the youngest of the study streams. Greater $\delta^{13}C$ enrichments in plane-bed morphologies has been observed (Sullivan 2013), and are most frequently occurring in SFC, less in WPC and IVS, and least in RPC and BBS.

Gende and Quinn (2006) found that insectivorous songbirds could be greater along streams supporting salmon, suggesting a response to increases in insect abundance. Changes in population dynamics due to MDN input can also contribute to a stronger impact into the surrounding environments, and could be expected to influence the older streams more than younger ones, which might have less structured systems and population responses to MDN. Hocking and Reynolds (2011) showed that MDN shifted plant community towards nutrient rich species, which in turn decreased plant diversity. Emerging insects could contribute large amounts of MDN to other areas of the watershed, and be incorporated into birds and other mammals like shrews and toads that utilizes them as prey. Francis et al. (2006) found emerging aquatic insects dispersing less than 0,03% of total nitrogen imported by spawning salmon. High $\delta^{15}N$ values found in adult Simuliidae suggests that emerging adult insects might represent more than a minor vector for salmon nutrients to the terrestrial environment in these watersheds. In the streams with lower mean $\delta^{15}N$ values (SFC, IVS and RPC), the Simuliidae adults actually had higher $\delta^{15}N$ values than larvae. This was the opposite in BBS and WPC, accommodating the largest pink salmon runs, were higher contribution of MDN affects their uptake of $\delta^{15}N$. Food web analysis may therefore be difficult to interpret with higher MDN input. This will likely vary greatly between the aquatic macroinvertebrates that emerge, but Simuliidae seem to be an important vector for dispersal of MDN into the surrounding terrestrial area. Densities of Simuliidae in WPC are very high, and could cover whole rocks and most of the bottom of the stream, and could be a significant vector in transporting MDN across boundaries. Wolf spiders were found to be the top predator in WPC, contributing to MDN transfer across environments.

4.4.3 Habitat variables, carbon and nitrogen

The physical habitat of the streams developed over time with increasing input for C and N sources. Older streams in Glacier Bay at higher elevations have smaller tributaries with more deciduous vegetation overhang, feeding the main stream channel. Most of the deciduous vegetation consists of alder (Alnus spp.) and willow (Salix spp.). Vogel and Gower (1998) found 33%–57% greater accumulation of C in the soil, in addition to greater C accumulation in aboveground vegetation when alder was present in the understory. Binkley et al. (1984) observed litter fall to be 3-7 times greater when Sitka alder was present, and could explain the higher C/N ratio in RPC and SFC. Ecosystem processes can be influenced by litter quality, and higher lignin concentration generally gives longer decay rates, and is related to decreased availability of total N (Scott and Binkley 1997). Triska et al. (1975) found that litter with lower C/N ratio decomposed faster and was a superior N source for aquatic invertebrates consuming litter detritus. The establishment of woody vegetation on gravel bars and floodplains is promoted by debris dams (Sidle and Milner 1989). Milner and Gloyne-Phillips (2005) found the cover of riparian vegetation to be positively correlated with lower bank stability, and established most rapidly in streams where downstream reaches where flow variation was buffered by a lake. Zhang et al. (2003) observed a significantly lower decomposition rate of alder leaves when adding salmon carcasses, due to a shift in the detrital consumer diet towards high nutrient resources. Vogel and Gower (1998) also found significantly more negative $\delta^{15}N$ values in alder and jack pine foliage when alder was present. High $\delta^{15}N$ levels in WPC is therefore expected to be mainly due to higher pink spawning abundance. Habitat differences and possible retention areas might influence the isotope levels found. Even if abiotic and biotic factors change with time, the different abiotic starting points for these streams after deglaciation will control much of the retention properties. Over time the influence from biotic factors increases, due to soil development and vegetation succession

(Milner et al. 2007). During several field seasons adult fish have not been observed in the IVS stream. Spawners have, however, been observed in and around the stream mouth waiting for water levels to rise. IVS was still the stream with highest observed 0+ coho densities in 2010. Since juvenile coho salmon is quite versatile, parts of the population might live in the estuaries during the winter period (Miller and Sadro 2003). We also observed coho 0+ salmonids in larger tidal pools 800-1500m away from the stream mouth. Alexander et al. (2000) found the rate of nitrogen-loss to decline rapidly with increasing channel size, and thus be of importance to the amount MDN retained in the streams.

4.4.4 MDN effect on instream salmonids

The influence of stream MDN on juvenile abundance and growth is more complex due to the retention and loss of MDN with stream age. Mean CPUE for both juvenile salmonids was negligibly influenced by MDN. However, the mean FL of juvenile Dolly Varden was related to pink salmon spawner abundance and mean $\delta^{13}C$, indicating that MDN influenced the growth thereby, partly confirming Hypothesis 3. This is early in the fall, and the MDN contribution and $\delta^{15}N$ and $\delta^{13}C$ levels will therefore be expected to be greater in the run. Scheuerell et al. (2007) found that the ration size and energy intake increased by 480-620% for both resident rainbow trout (*Oncorhynchus mykiss*) and Arctic grayling (*Thymallus arcticus*) following sockeye salmon spawning. Juvenile Dolly Varden FL also showed a directional relationship with $\delta^{13}C$, implying food sources related to spawning pink salmon to be more important for juvenile Dolly Varden than juvenile coho salmon. Juvenile coho salmon FL showed a directional relationship with total C, likely less connected to spawning salmonids, as were found in chapter 3 to consume larger amount of terrestrial invertebrates. The results here show that the range of %N and C% is more important in relation to mean CPUE and FL for juvenile coho salmon.

4.4.5 MDN fluxes.

The MDN influence will be a result of pink salmon contribution and the physical habitat. Mean $\delta^{15}N$ and $\delta^{13}C$ and $\delta^{15}N$ and $\delta^{13}C$ SD show relationship, and significant for carbon, showing increased $\delta^{15}N$ and $\delta^{13}C$ lower the discrimination of the overall stream biota. This since variance of $\delta^{13}C$ should imply larger variation in food source, and the smallest variation was found in WPC which supported the largest pink salmon abundance. One should therefore be cautious when using $\delta^{15}N$ and $\delta^{13}C$ analyses without taking into account the sampled environment, and the fractioning of $\delta^{15}N$ and $\delta^{13}C$. While the dispersion of %N SD was more similar to dispersion of $\delta^{15}N$ SD, the range of %N followed more the range of %C, indicating the range to be more connected to the physical habitat of the stream. The CPUE and FL of juvenile coho also showed a significant connection to %N range. While this study focused on salmon contribution, the stream %N and %C range is low in WPC due to high salmon abundance. The %N and %C range are higher in IVS and BBS, suggesting that the physical habitat influences distribution and availability of elements. Differences in stream biota $\delta^{15}N$ and $\delta^{13}C$ levels are affected by many factors, both abiotic and biotic. Koshino et al. (2013) found $\delta^{15}N$ and $\delta^{13}C$ isotopes in aquatic organisms increased 1–4‰ and 1–6‰ respectively after the arrival of returning salmon. Micro and macro-invertebrates, as well as mammals and birds, are vectors from ocean via streams to terrestrial environments, and help accumulate MDN over time. Alexander et al. (2000) found a rapid decline in nitrogen loss with increasing stream channel width and depth. Female arctic charr (*Salvelinus alpinus*) lost approximately 80% of their body lipids during spawning and overwintering (Jørgensen et al. 1997), and would most likely increase the $\delta^{13}C$ and $\delta^{15}N$ availability in the streams and lower the discrimination against $\delta^{15}N$ and $\delta^{13}C$ (Caut et al. 2008). Discrimination of $\delta^{13}C$ during lipid biosynthesis varies with stable isotope dietary concentrations (Wessels and Hahn 2010). The tissue variations in $\delta^{13}C$ and the large seasonal variations of lipids (Jørgensen et al. 1997) need to be addressed when undertaking isotopic sampling. Demanding an even larger sample

size to account for the large variation between individuals, and multiple sample times to account for the variation in growth and change in development and seasons. Yoshimura (2015) suggests that value gaps in $\delta^{15}N$ and $\delta^{13}C$ can be used to assess biodiversity and give indications for biodiversity estimations in a stream. Results indicate on the other hand that the diversity could due to larger variation in isotopic $\delta^{15}N$ and $\delta^{13}C$ abundance or a resource depression. Use of other isotopes like $\delta^{18}O$, $\delta^{2}H$ and $\delta^{34}S$ can aid to a better understanding of food web dynamics, nutrient transports and population migrations. Hansen et al. (2009) showed the potential of $\delta^{34}S$ in combination with $\delta^{15}N$ and $\delta^{13}C$ to improve discrimination of food sources in aquatic food webs. Analyzing the content of lipids in the samples seems to be a more rigid way, in order to avoid loss and change in sample element composition, in addition to help establish the samples nutritional value. While pink salmon spawning was the main vector for MDN into aquatic, semi-aquatic and terrestrial environments in Glacier Bay streams, many other pathways and vectors exist (mammals and birds) for spreading the MDN from the aquatic stream system and onwards into the terrestrial environments in each watershed. Both adult Simuliidae and wolf spiders showed high levels of MDN and provide a continuous flux of MDN across environments. A directional relationship of range and SD of $\delta^{15}N$ and $\delta^{13}C$ indicate the importance of age in how MDN would be available to stream biota. Alexander et al. (2000) found far-reaching dendritic streams to contribute the most nitrogen to the river inlet. While this describes the change with age through dispersion of $\delta^{15}N$ and $\delta^{13}C$, there are limitations in interpreting the accumulation, loss and the effect on juvenile salmonids. Especially since measurements were only undertaken at one time during the year and at one reach of the stream. While the pink salmon abundance gives indications of $\delta^{15}N$ levels, all of the spawner activity should be accounted for to make a good prediction of their effect. The range of %N and %C warrants further research, and should include the range of %P, since variation in %N, %C and %P influences juvenile coho salmon significantly. Since only one reach were sampled in 2011, replicate samples should be taken throughout the watershed in order to assess the effect of salmon spawners and the temporal effect of accumulation.

4.5 Conclusion

The chronosequence found in Glacier Bay, due to glacier retreat, creates a unique opportunity to study newly developed streams and the influence of MDN as streams increase in complexity with watershed development. Findings indicated that mean $\delta^{15}N$ within stream biota increased with stream age, likely as a result of higher retention of MDN with increasing stream complexity. Dispersion increased with steam age for both $\delta^{15}N$ and $\delta^{13}C$, as watershed development increases carbon and nitrogen availability in the streams. This dispersion also masked the possible accumulation of MDN in the streams due to increased discrimination of $\delta^{15}N$ and $\delta^{13}C$. These findings raises questions about food web analysis, as the range of $\delta^{15}N$ and $\delta^{13}C$ will influence the $\delta^{15}N$ and $\delta^{13}C$ levels, and consequently the food webs and trophic niche width based solely on $\delta^{15}N$ and $\delta^{13}C$. The results suggest that the discrimination of $\delta^{15}N$ and $\delta^{13}C$ are based on variation of carbon and nitrogen in the streams. This is important when interpreting trophic community length and diversity of basal resources, as this could explain nutrient availability, instead of giving an indication of high diversity. This would then mean less energy availability or a resource depression (confirmed in chapter 3 through diet analysis). This study focused on salmon contribution, and shows stream %N and %C range to be low in WPC due to high salmon abundance. Accumulation of MDN as a feature of time (age) could lead to the assumption that age is a continuous factor in how much MDN is retained or lost in the different streams. Pink salmon spawner abundance is the most important factor in delivering MDN due to their much higher numbers compared to other spawning salmonid species, a stronger connection between stream biota and pink salmon spawners would therefore be expected later in the fall. The annual boost of MDN due to returning salmonids is important to maintain and accumulate MDN, while the retention properties will increase the amount of MDN stored in the watersheds. Combining enumeration of salmon spawners with stable isotope sampling before and after spawning helps to assess the retentive properties of the streams, and also the temporal effect on MDN accumulation within the stream. Morphological features should be included when investigating watershed retention

properties. This will enhance our understanding of salmonid ecology and can be used to calculate an accurate stream bearing capacity for juvenile salmonids. Further research is required to understand the different pathways of MDN into aquatic systems and changes in nutrient retention with complexity, and are important in river restoration. The possibility to start measuring MDN in a newly colonized stream and its temporal impact will increase knowledge of MDN contribution to the various environments and how they are influenced by this nutrient flux.

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4.7 Table and Figures

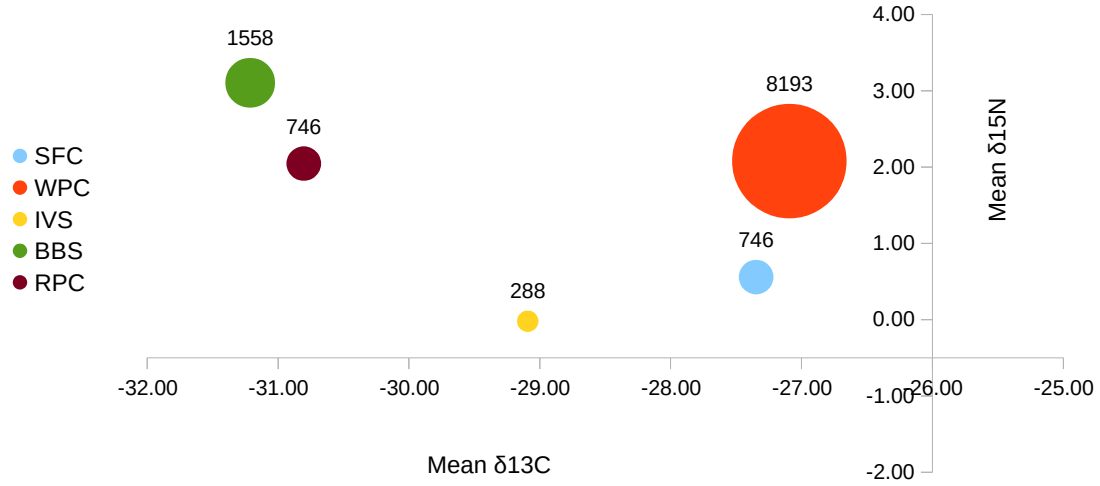

Figure 4.2: Mean $\delta^{13}C$ and $\delta^{15}N$ stream levels (2011) and mean pink salmon spawner abundance (2009-2011).

Table 4.1: Stream age, isotope measurements, SD, ranges, pink salmon counts and juvenile FL, CPUE.

		Streams				
Stream age and means, SD, and range	**PCA**	SFC	WPC	IVS	BBS	RPC
Age	a	39	65	141	181	206
Mean $\delta^{15}N$	b	0.56	2.08	-0.02	3.10	2.05
Mean $\delta^{13}C$	c	-27.35	-27.09	-29.09	-31.21	-30.80
Mean %N	d	8.70	8.55	8.64	8.58	8.88
Mean %C	e	42.78	42.98	42.68	41.51	43.10
Mean C/N ratio	f	9.73	8.80	9.30	9.01	10.35
$\delta^{13}C$ SD	g	1.45	1.80	2.98	4.05	4.17
$\delta^{15}N$ SD	h	3.40	2.89	3.73	3.76	4.00
%C SD	i	11.77	11.44	13.17	12.69	11.83
%N SD	j	5.14	4.89	5.10	5.12	5.22
$\delta^{13}C$ range	k	6.64	6.86	10.32	13.48	14.29
$\delta^{15}N$ range	l	11.97	10.28	12.88	11.23	11.88
%C range	m	44.93	43.76	48.00	47.44	47.36
%N range	n	14.30	14.28	14.58	14.51	14.34
Mean pink salmon counts	o	746	8193	288	1558	747
Mean FL juvenile coho salmon	p	72.03	70.88	66.18	63.70	69.96
Mean FL juvenile Dolly Varden	q	97.58	111.95	102.34	80.03	81.30
Mean CPUE juvenile coho salmon	r	11.81	8.38	3.13	5.30	11.73
Mean CPUE juvenile Dolly Varden	s	2.83	2.45	2.13	1.13	5.19

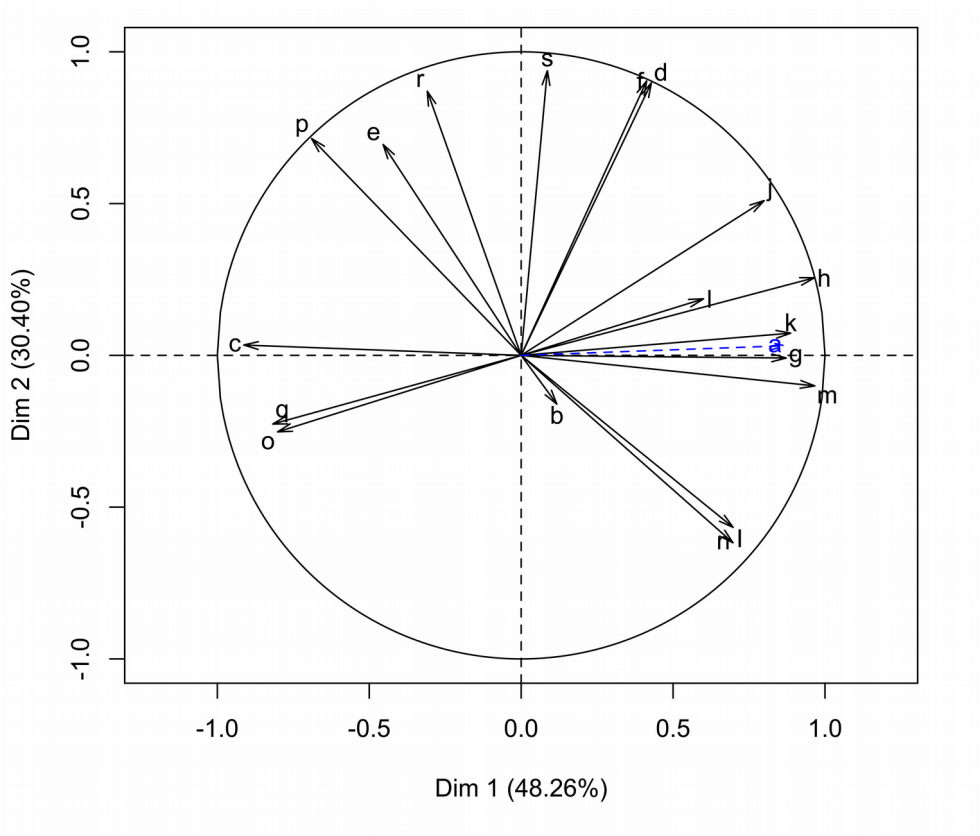

Figure 4.3: PCA biplot and the directional relationships between three year mean juvenile coho and Dolly Varden CPUE and FL, mean pink salmon counts, age and MDN.

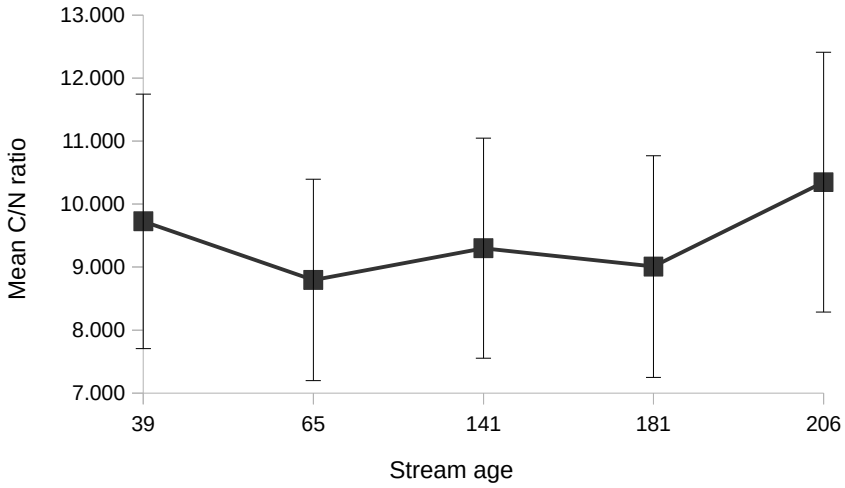

Figure 4.4: Mean C/N ratio ±1SE for each stream.

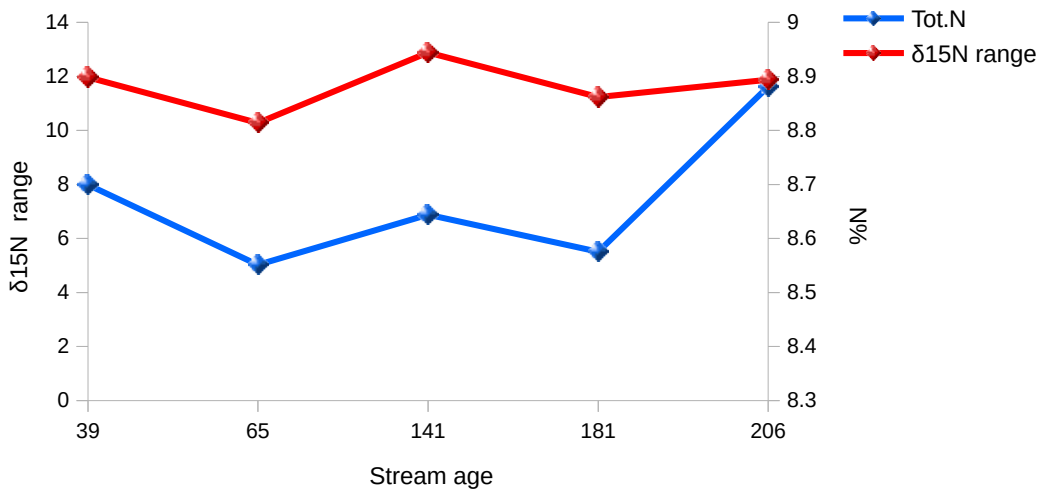

Figure 4.5: Mean %N and δ^{15}N range in the biota per stream.

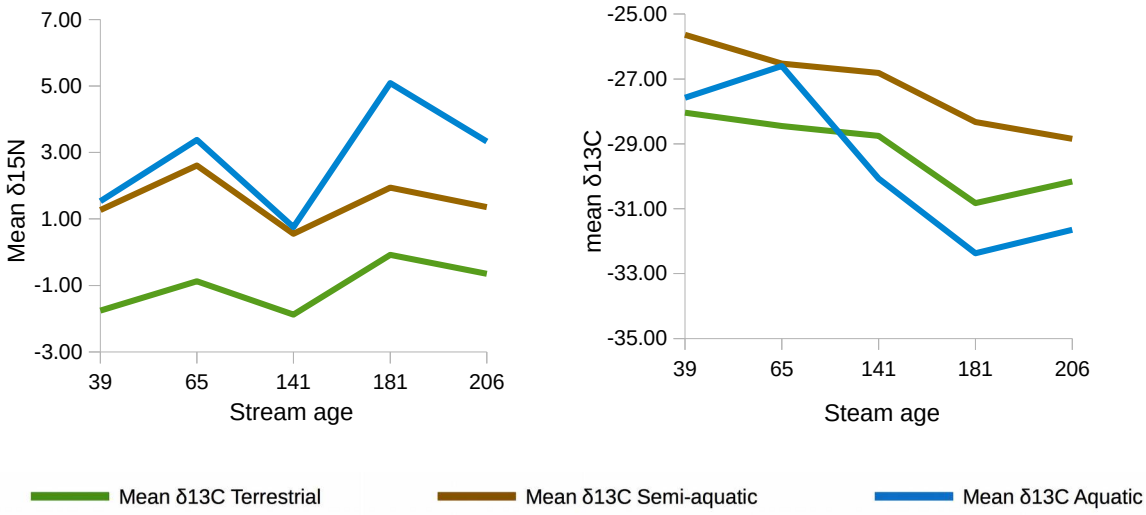

Figure 4.6: Mean δ^{15}N a) and mean δ^{13}C b) in terrestrial, semi-aquatic and aquatic environment

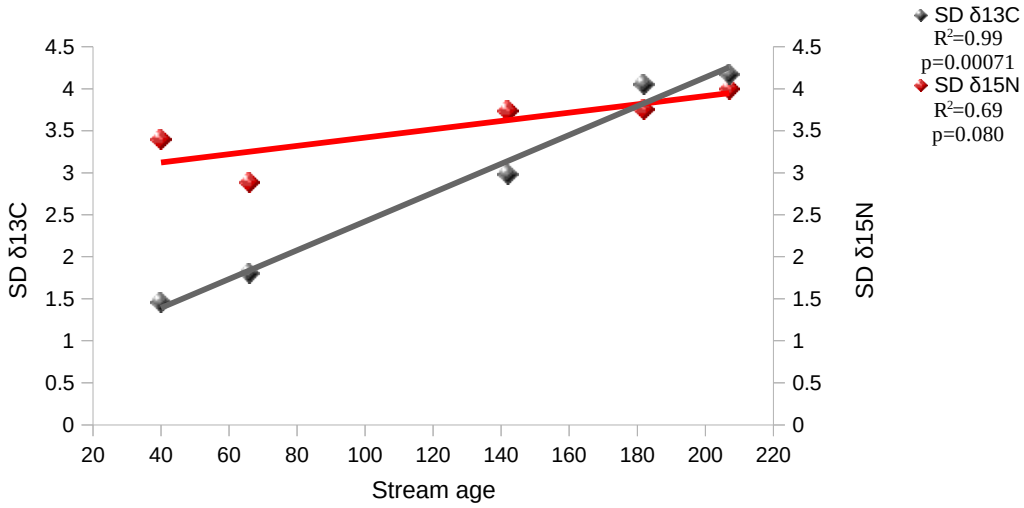

Figure 4.7: Standard deviation (SD) as a function of stream age for $\delta^{15}N$ and $\delta^{13}C$.

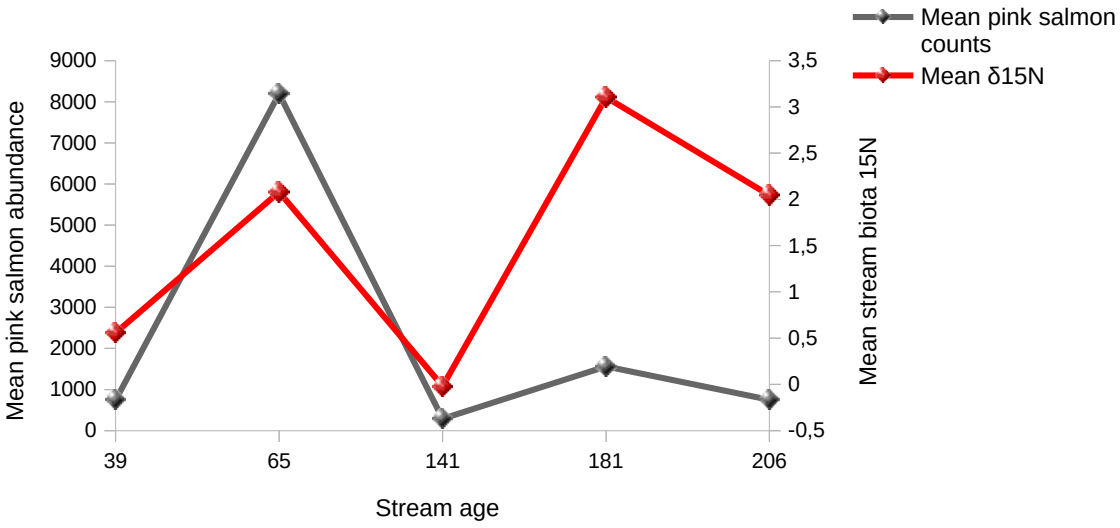

Figure 4.8: Mean pink salmon abundance and mean $\delta^{15}N$ biota per stream.

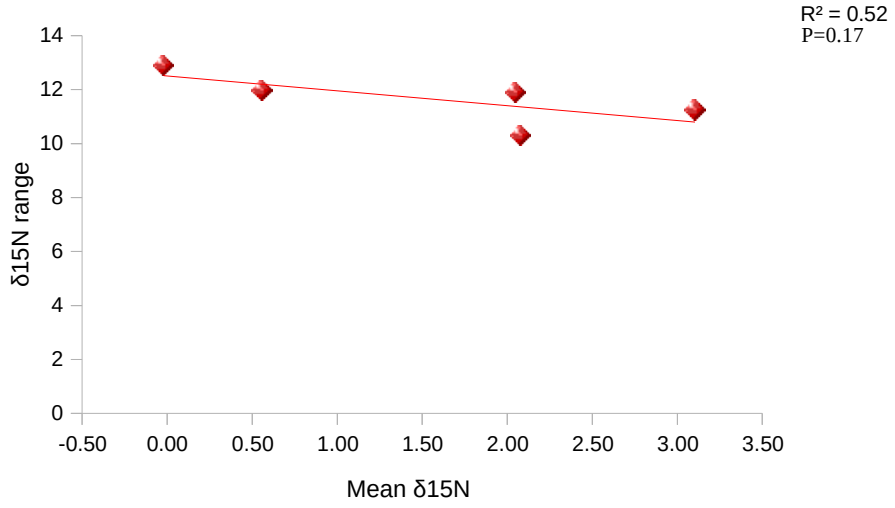

Figure 4.9: Mean $\delta^{15}N$ and $\delta^{15}N$ range in the biota per stream.

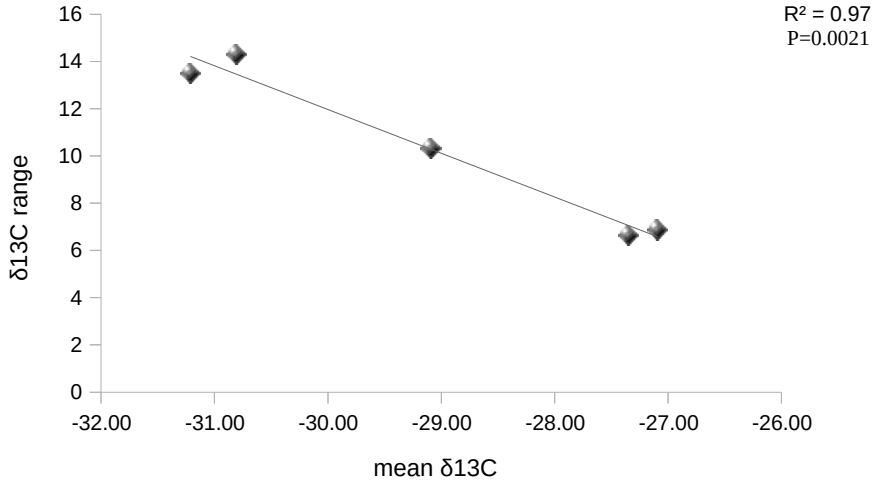

Figure 4.10: Mean $\delta^{13}C$ and $\delta^{13}C$ range in the biota per stream.

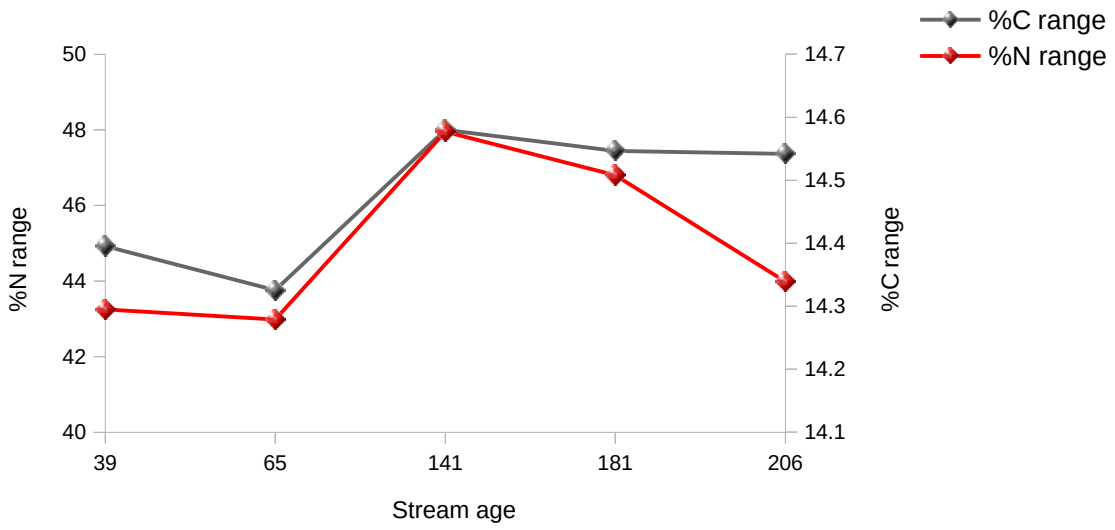

Figure 4.11: %N and %C range in the biota per stream.

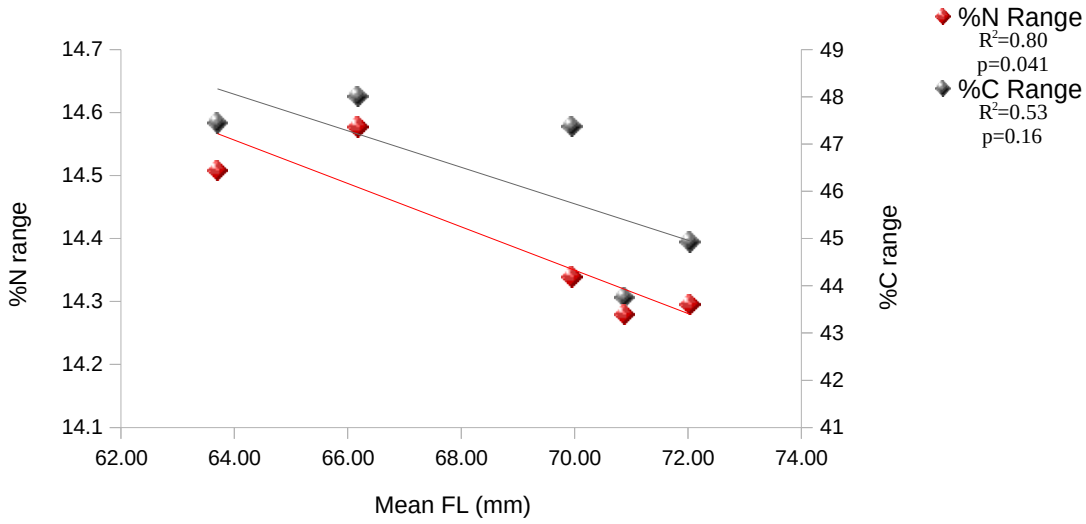

Figure 4.12: Mean FL juvenile coho salmon and %N and %C range in the biota per stream.

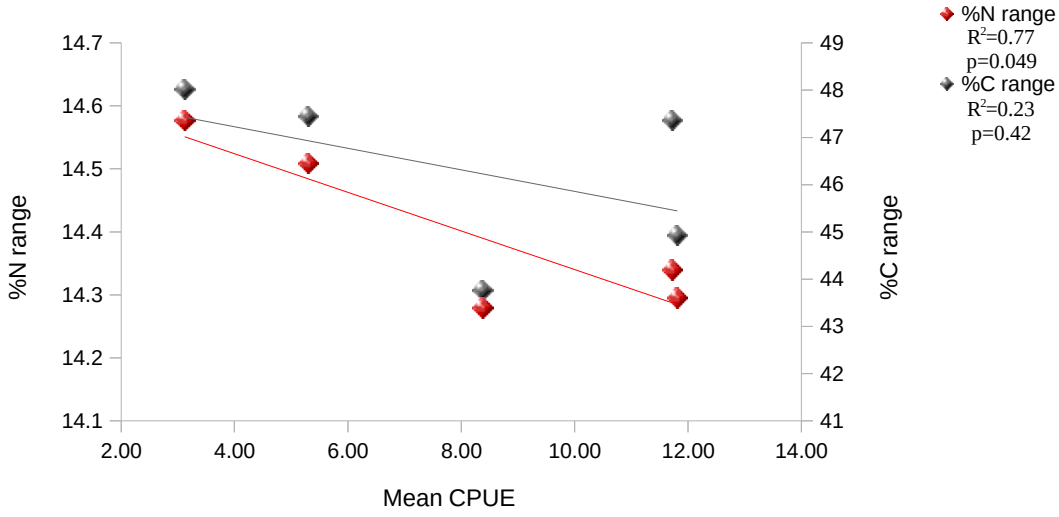

Figure 4.13: Mean CPUE juvenile coho salmon and %N and %C range in the biota per stream.

5. Sea lice (Lepeophtheirus salmonis) as a food source for juvenile salmonids in southeast Alaska.

Abstract

Sea lice (*Lepeophtheirus salmonis*) are an obligate marine macroparasite commonly found on Pacific salmonids, and typically die shortly after spawning salmon enter freshwater due to its stenohaline restriction. Sea lice were found to be a food source for juvenile salmonids in streams of Glacier Bay, in southeast Alaska. Sea lice abundance in the diet of juvenile coho salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*) were strongly correlated with salinity in the surface waters in Glacier Bay, with a notable absence of sea lice in the diet of juvenile salmonids in younger streams in the upper bay. Pink salmon (*Oncorhynchus gorbuscha*) were the most important vector for sea lice reaching freshwater systems. To our knowledge this is the first documentation of sea lice in the diets of juvenile salmonids thereby suggesting another route of marine derived N, P and C contribution to stream food webs.

5.1 Introduction

Sea lice (*Lepeophtheirus salmonis*) are a marine ectoparasitic copepod commonly found in the Northern Hemisphere (Connors et al. 2008b), one of several *Lepeophtheirus spp*. While typically associated with anadromous salmonids, several non-salmonids can act as hosts (e.g. the three spine stickleback (*Gasterosteus aculeatus*)). In this paper *Lepeophtheirus salmonis* will be referred to throughout as sea lice. The extent of infestation varies between species, life stage, habitats and temporally in marine waters (Wertheimer et al. 2003, Trudel et al. 2007). Jones et al. (2006) found variation in sea lice development on threespine stickleback juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbuscha*) in the coastal waters, with mean abundance of sea lice significantly higher on threespine sticklebacks. Prevalence and abundance increased with host size and ocean age and approximately 90% of the total number of parasites occurred on pink and chum salmon (Nagasawa 1987). Nagasawa (2001) found sea lice infections to vary among adult salmon hosts, with pink and chum salmon accounting for 87% of the sea lice population from 1991 to 1997. Sea lice prevalence on adult salmon varied from 33.3% on chum salmon to 71% on pink salmon, and to vary 100% on coho salmon in neritic waters south of Glacier Bay (Wertheimer et al. 2003). Juvenile pink salmon (2.9%), juvenile chum salmon (4.2%) and outmigrating juvenile sockeye salmon (*Oncorhynchus nerka*) (8.4%) had low prevalence, whereas outmigrating juvenile coho salmon smolts showed a high prevalence of 53.2% in the Icy Strait (Wertheimer et al. 2003).

Sea lice have eight life stages; two nauplii, one copepod, two chalimus, two pre-adult and one adult (Hamre et al. 2013). The nauplii stage is non feeding planktonic larvae, an infective planktonic copepod stage, chalimus stage embedded on the host skin and mobile pre-adults and adults that can move freely over the host skin (Hamre et al. 2013). Development time and survival are strongly influenced by water temperature and salinity (Johnson and Albright 1991), and (Jones et al. 2006) found increased salmon size was associated with decreased

louse abundance and increased louse development. Sea lice copepodids in the sea is suggested to aggregate in vicinity of steep salinity gradients (Heuch 1995). Mennerat et al. (2012) observed a negative correlation between average sea lice fecundity and fish growth, and found area of skin damage to decrease over time, while found to increase with infestation intensity. Higher levels of host immunity response might slow development and reduce the fecundity of sea lice (Mennerat et al. 2012). Survival and host infectivity of sea lice are greatly reduced by short-term exposure to low salinity (Bricknell et al. 2006). Connors et al. (2008b) observed no sea lice survival after 108h in fresh water, and no significant variation in survival between sexes. While adult sea lice survival in freshwater varies, survival has been reported up to 3 weeks on Arctic charr (*Salvelinus alpinus*) (Finstad et al. 1995). Fish are likely to return to fresh water in order to restore compromised osmotic imbalance (Bjørn et al. 2001), and delouse in the process (Finstad et al. 1995).

The natural abundance of sea lice, Caligidae family, is not well known, as most research is related to aquaculture, as their most significant pathogen, which is estimated to cost the world fish industry €300 million a year (Costello 2009). Bjørn et al. (2001) observed significantly higher sea lice infections at locations with salmon farming. Natural background levels of sea lice are therefore important to understand the negative influence of salmon farms. Salmonids in Alaska have no problems with the natural sea lice populations, as there are no fish farms (net-pens) that could increase their abundance. Sea lice abundance in Glacier Bay are only 0-4 per fish according to C Soiseth (personal communication 2014).

The principal aim of this study was to examine the diet of juvenile coho salmon and Dolly Varden with relation to watersheds at different stages of development since deglaciation and potentially different food sources. All five streams studied support pink, chum and coho salmon and Dolly Varden, and a few streams also accommodate sockeye runs. Glacier Bay is a unique natural laboratory for studying colonization and succession of stream systems, and the fjord provides a strong salinity gradient where the natural abundance of sea lice can be

studied. Salmon are keystone species and constitute links between marine and terrestrial habitats (Orsi et al. 2002). These results elucidate the abundance of sea lice found in the diet of stream-dwelling juvenile coho salmon and Dolly Varden, and the relation to the salinity gradient found from younger to older watersheds due to deglaciation.

5.2 Methods

5.2.1 Study area

The study was undertaken within Glacier Bay National Park in southeast Alaska, consisting of a fjord with two major arms, and have experienced glacial retreat since the Little Ice Age maxima in 1760. During deglaciation of Glacier Bay, watersheds and streams have emerged with different age and complexity. Five streams were examined; Stonefly Creek (SFC), Wolf Point Creek (WPC), Ice Valley Stream (IVS), Berg Bay South Stream (BBS), and Rush Point Creek (RPC) ranging from 39 to 206 years since the stream mouth was revealed. Determination of stream age used satellite and aerial photos, historical data, journal articles and unpublished data, as outlined in (Milner et al. 2000). Figure 5.1 show the study streams in Glacier Bay National Park and the CTD (Conductivity, Temperature, Depth) stations.

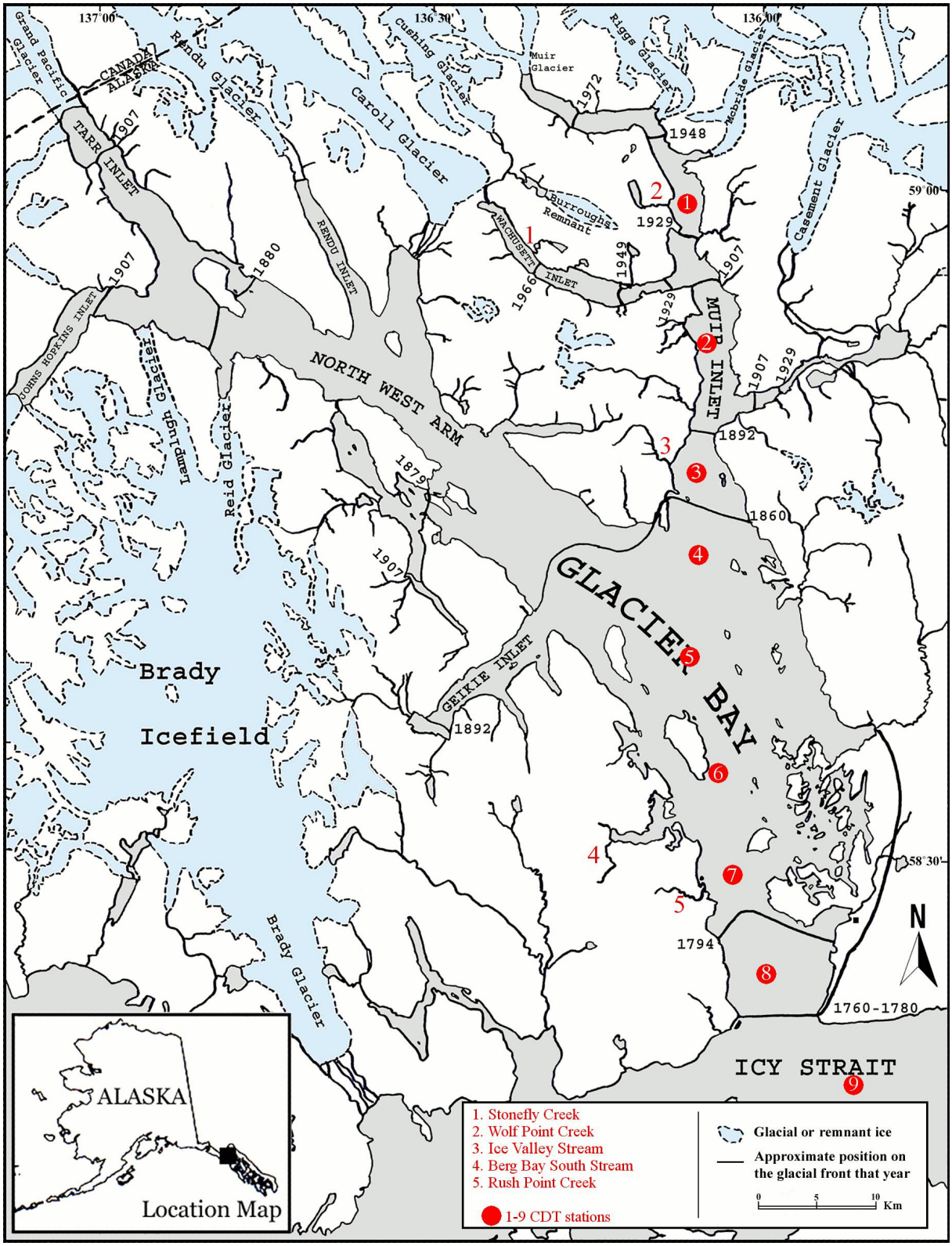

Figure 5.1: Map of the study streams and CTD stations.

5.2.2 Sample collection

Juvenile coho salmon and Dolly Varden char were captured in minnow traps (400mm x 220mm, with a 6mm mesh), baited with salmonid eggs soaked in iodine. Minnow traps were fished for 1.5h at each site between Jul 28th- Aug 14th in 2009, 2010 and 2011. In 2011, eggs were enclosed inside "Kinder egg" capsules with small holes to prevent juvenile salmonids consuming the eggs. Captured juvenile coho salmon and Dolly Varden were sedated with clove oil, their guts evacuated and stored in 70-80% ethanol. At the laboratory stomach contents were examined under a stereo-microscope, and clearly identifiable material counted.

Water temperature and salinity measurements of the fjord were undertaken by the U.S. National Park Service from 2009 to 2011 in mid July at 1 m increments. Nine measuring stations were located from the upper fjord, parallel to WPC, southwards to Icy Strait, which correlates best with our streams. The sampling were undertaken during a period when Glacier Bay would be expected to contain migrating adult salmonids returning to spawn. CTD stations are marked in Figure 5.1. MATLAB was used to create the salinity contours by depth, and distance from station 1 to 9. Salinity PSU (Practical Salinity Unit) was measured from 1 to 40m, as most Pacific salmonids utilize these ocean depths (Walker et al. 2007, Morita 2011). Correlation between sea lice abundance in the guts of stream dwelling juvenile coho salmon and Dolly Varden (2009-2011) and salinity (2009-2011), was performed in R v3.1.2 (GUI 1.65). Pink salmon spawner abundance was estimated by averaging the counts of two observers walking the length of the stream.

5.3 Results

Sea lice were found in the stomachs of juvenile coho salmon and Dolly Varden in the lower older bay streams BBS and RPC, but not found in the diet of juvenile salmonids in the upper bay streams, IVS, WPC and SFC (Table 5.1). Mean sea lice occurrence (2009-2011) in the diet correlated significantly with mean salinity at 1m in mid July (Correlation coefficient = 0.89, p = 0.040) (Figure 5.2). Salinity and water temperature contours are displayed in Figure 5.3 with distance in km from CTD station 1 in the upper bay to CTD station 9 in Icy Strait. Salinity increased from the upper east-arm southwards to Icy Strait, varying at 1m from 12.82 PSU to 30.98 PSU from 2009-2011 from upper bay outside WPC to Icy Strait, with higher gradient in 2009 and 2010. CTD station number 2 was the closest to SFC, and showed the lowest mean salinity (2009-2011) at 1m with 15.9 PSU. Glacier Bay has a strong tidal activity, but freshwater is notably in the upper east arm, close to glacial influence. Surface water temperature was higher and salinity was lower in 2010 compared to 2009-2011. Significantly higher abundance of sea lice were found in 2009 and 2011 (21 and 56). In contrast in 2010 only 2 sea lice were found in the stomachs of fish from RPC, and none in BBS. Only female sea lice were observed in the diet of juvenile salmonids. In RPC 2011, both juvenile coho salmon and Dolly Varden consumed more sea lice than salmon eggs. Although only around 150 adult pink salmon were enumerated on August 8th 2011, 50 sea lice were found in the guts of 7 juvenile coho and 8 juvenile Dolly Varden. Over 1100 adult pink salmon were counted in BBS on August 9th 2011, and 11 sea lice were found in the diet of 3 coho and 5 Dolly Varden.

Table 5.1: Percent juvenile salmonids with sea lice in the diet, and range of sea lice found per fish 2009-2011.

Stream	Salmonid	Year					
		2009		2010		2011	
		% (Range)	Fish (n)	% (Range)	Fish (n)	% (Range)	Fish (n)
SFC	Juvenile coho salmon	0	30	0	30	0	30
	Juvenile Dolly Varden	0	29	0	30	0	30
WPC	Juvenile coho salmon	0	28	0	26	0	30
	Juvenile Dolly Varden	0	23	0	2	0	21
IVS	Juvenile coho salmon	0	30	0	32	0	30
	Juvenile Dolly Varden	0	24	0	2	0	30
BBS	Juvenile coho salmon	30% (0-4)	30	0	24	10% (0-1)	30
	Juvenile Dolly Varden	60% (0-3)	5	0	13	16,6% (0-3)	30
RPC	Juvenile coho salmon	3.33% (0-1)	30	0	30	22.58% (0-5)	31
	Juvenile Dolly Varden	3.4% (0-1)	29	6.66% (0-1)	30	26,6% (0-11)	30

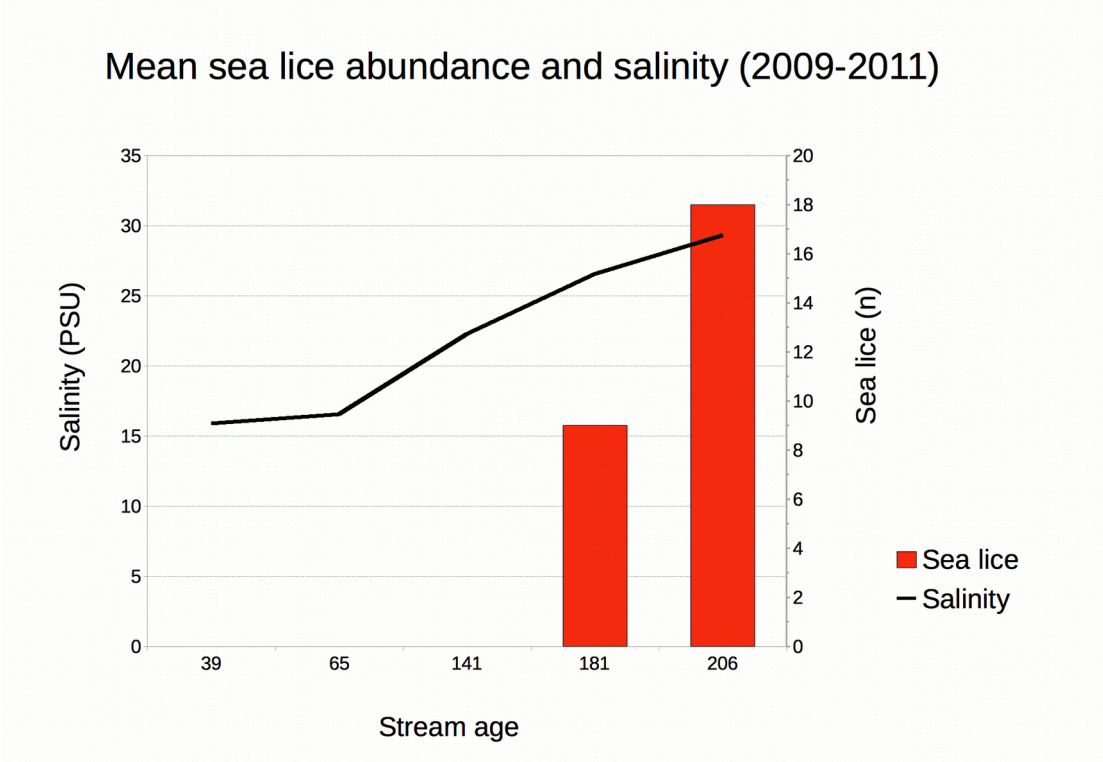

Figure 5.2: Mean abundance of sea lice in the stomachs of juvenile coho salmon and Dolly Varden and mean salinity (n = 3 years).

a) b)

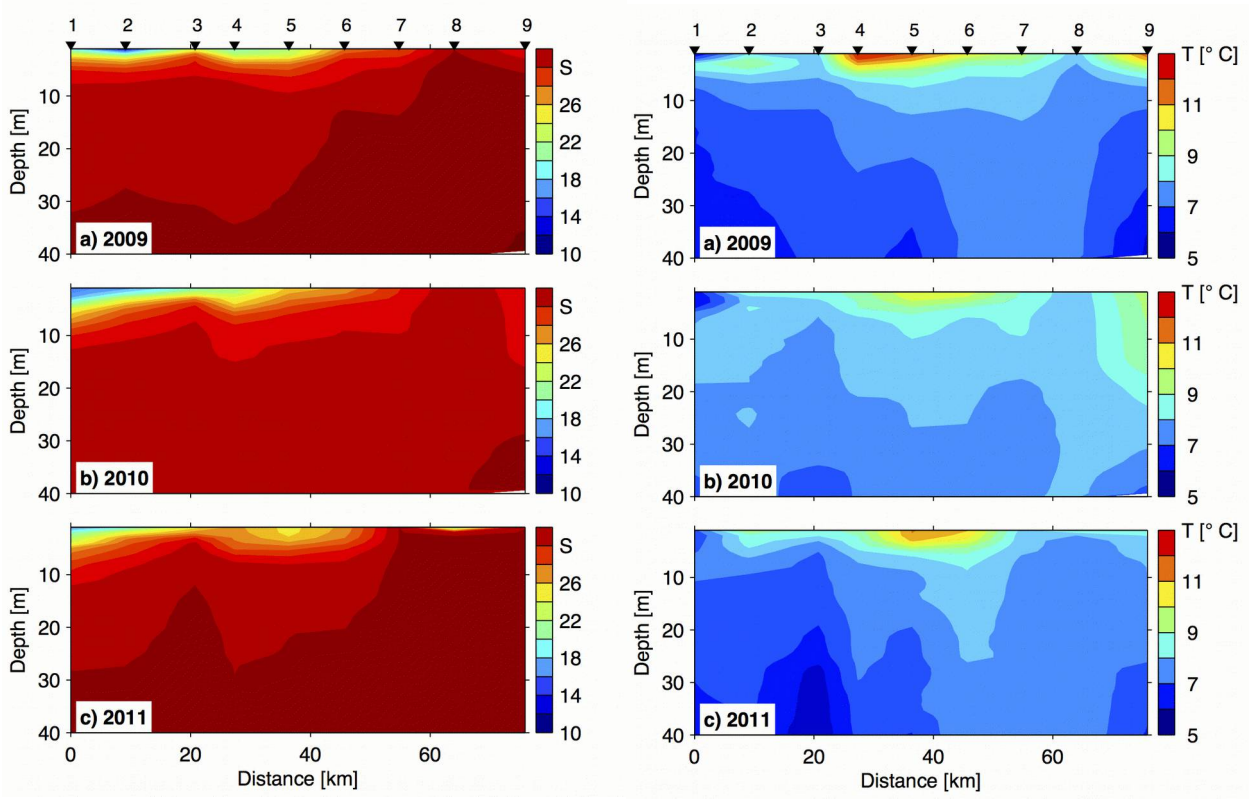

Figure 5.3: (a) water temperature and (b) salinity to a depth of 40m at CTD station 1-9.

5.4 Discussion

The increasing salinity gradient from the upper to lower bay streams would account for the difference in sea lice occurrence in the stomachs of juvenile salmonids. Sea lice were not found in juvenile salmonids in streams entering the fjord where salinities were < 25 PSU, indicating that adult salmon are free of sea lice before entering these natal streams. The capability of sea lice to remain attached to adult salmon is reduced in the upper bay areas due to lower salinities in the surface water. Tanaka et al. (2000) found a positive correlation between 0-1m surface water swimming chum and cool surface water, which may lead to a higher loss of sea lice, due to prolonged time in low salinity water. Jones et al. (2006) observed a spatial relationship between sea lice abundance and the salinity of the surface water. Surface water salinity further south between IVS and BBS streams changed notably, with waters proximal to BBS and RPC > 25 PSU. Lower water temperature in surface water in 2010, could, in addition to lower salinity, be considered to reduce the influence of sea lice in the lower bay streams that year. The large difference in pink salmon spawners would be the main reason in making sea lice available to stream-dwelling salmonids. Scaling has been observed in other studies (Wertheimer et al. 2003), and is occurring naturally when salmon are jumping. Furevik et al. (1993) observed greater jumping activity with increased louse infestation on Atlantic salmon (*Salmo salar*) in net pens. Sea lice scaling in Glacier Bay would likely be enhanced by the substantially lower salinity in the surface water.

Higher abundance of sea lice in the diet of juvenile coho salmon and Dolly Varden in 2009 and 2011 compared to 2010 is linked to the higher odd year size of pink salmon runs, as pink salmon have been found to be one of the most important host for sea lice (Nagasawa 1987, 2001, Nagasawa and Takami 1993). Nagasawa (2001) found sea lice population fluctuations to be synchronized with the annual abundance of pink salmon. Wertheimer et al. (2003) found sea lice population decreases in strait habitats from August, which could be due to juvenile migration away from these habitats. The sea lice on later returning salmon can as a

consequence stay attached longer due to fewer suitable host in the strait after juvenile salmon migration. Johnson and Albright (1991) found that early and infective stages were most sensitive to low salinity, and sea lice copepodids survived for < 24h at ≤ 10‰ salinity.

Fish gut samples were collected at the beginning of the pink salmon runs, and a higher content of sea lice in the diet could be expected at the peak of pink salmon run. Coho and chum salmon run later in the year, and with salinity gradually increasing in the 2m surface water throughout September (Orsi et al. 2002), could lead to a higher number of sea lice still attached when salmon reach their natal stream. Due to the low numbers of these species compared to pink salmon their overall contribution will be low. Time of salmon runs varies from year to year, often regulated by stream water level. Sampling time could therefore contribute to a variance in the sea lice availability. Sea lice abundance in the stomachs of juvenile salmonids is expected to be greater later in the fall, due to higher pink salmon abundance and other Pacific salmonids spawning later in the fall.

The route of sea lice being incorporated into the diets of juvenile salmonids is unknown. Mortality may occur or detachment from the adult salmon and then consumed from the drift or directly removed by the juvenile salmonids from adult fish. However due to mortality when entering freshwater, scaling when salmon dig redds and competition for spawning sites, diet contribution through drift seems the most probable route. Experimental studies have found that sea lice tend to become detached from their host over time (Finstad et al. 1995). Connors et al. (2008b) expected missing sea lice on juvenile pink and chum salmon during the experiment were to be eaten by the host after falling off, while (Morton and Routledge 2005) observed that the juvenile pink and chum salmon picked adult sea lice off each other.

Only adult female sea lice were found in the stomachs of juvenile coho salmon and Dolly Varden, possibly due to a difference in behavior and morphology constraining escape (Connors et al. 2008a) from adult salmon entering natal streams. Hull (1998) observed that

the mean adult male sea lice inter-host transferrers were approximately 3.5 times greater than in mated females, and that transferring males tended to transfer more often. Sea lice also escape host predation by moving from prey to predator, and male sea lice were found to transfer 3.8 times more frequently than females (Connors et al. 2008a). Males can mate several times and make no further investment in the fertilized progeny (Hull 1998). Males would be expected to already be detached when adult salmon enter freshwater. Juvenile salmonid numbers were generally highest in the strait habitats in southeastern Alaska (Orsi et al. 2002), where salmonids pass during their homing migration. This could lead to a loss of adult sea lice to juvenile salmonids, especially for males. Female sea lice were more common in the guts than eggs in RPC in 2011, which was unexpected due to the low overall prevalence of sea lice in Glacier Bay. While attached sea lice could last for more than a week in fresh water when still attached, they will succumb after 8 hours if free swimming (Hahnenkamp and Fyhn 1985). The time spent in the fjord could be important to the number of sea lice that still would be attached when adult salmon enter their streams and become available to in-stream juvenile coho and Dolly Varden.

Salmon returning to spawn have an important role in the contribution of marine derived nutrients (MDN) to their natal streams as they accumulate 95% of their biomass in the ocean (Schindler et al. 2003). Stable isotope analyses of adult female sea lice show high δ15N levels, all above >13‰. Dean et al. (2011). Sea lice contribute MDN, as well as nutrient value due to their physically large size, compared to other in-stream diet items. Another study shows that Pacific salmon eggs accounted for at least 90% of the October diet of instream salmonids, and appeared responsible for a large increase in condition factor (Johnson and Ringler 1979). Sea lice could play an important role in the diet of juvenile coho salmon and Dolly Varden. The spatial diet difference of sea lice in the diet observed between upper and lower bay could potentially enhance the condition factor of these salmonids.

5.5 Summary

To our knowledge sea lice as a food source for stream-dwelling juvenile salmonids has not previously been documented. Salinity in estuarine and proximal waters to watersheds plays an important role in determining whether sea lice enter freshwater, possible in synergism with lower surface water temperatures due to meltwater and glacial runoff. This occurrence illustrates another route by which MDN can become incorporated into stream food webs and may enhance fish condition when available.

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6: Synthesis

6.1 Introduction

The research presented in this thesis concerns the study of interactions with colonizing salmonid populations in watersheds of different ages following glacial recession.

Interferometric synthetic aperture radar (IFSAR) data of the study streams was analyzed with geographic information systems (GIS) to identify important variables to create physical habitat template's (PHTs) of the watersheds, in order to quantify change following glacial retreat (Chapter 2). The diet of juvenile coho salmon and Dolly Varden in streams of different age and complexity was examined, and how growth was affected by which food sources that were consumed (Chapter 3). The contribution of marine derived nutrients (MDN) from pink salmon spawners was examined in the context of the change in isotopic $\delta^{15}N$ and $\delta^{13}C$ with age of the watershed (Chapter 4). Sea lice were for the first time documented in the diet of juvenile salmonids. This occurred in the older streams due to higher salinity in the lower part of the fjord where their estuaries were found (Chapter 5). The diet findings from the two species are linked to the PHT analysis to create "landscape of salmonid populations", where the initial PHT controls the colonization and dynamics of juvenile salmonid population development and influences their diets (Chapter 6).

The findings are combined and presented here to provide an understanding of the interconnectedness of stream development with other ecosystems after glacial retreat, and to examine the impact of the major linkages among stream, lake, terrestrial and marine intertidal environments at Glacier Bay proposed by Milner et al. (2007). The initial watershed PHT after deglaciation determines the physical abiotic variables and associated habitat response which has major influence on the future development. Major linkages proposed by Milner et al. (2007) are shown in Figure 6.1.

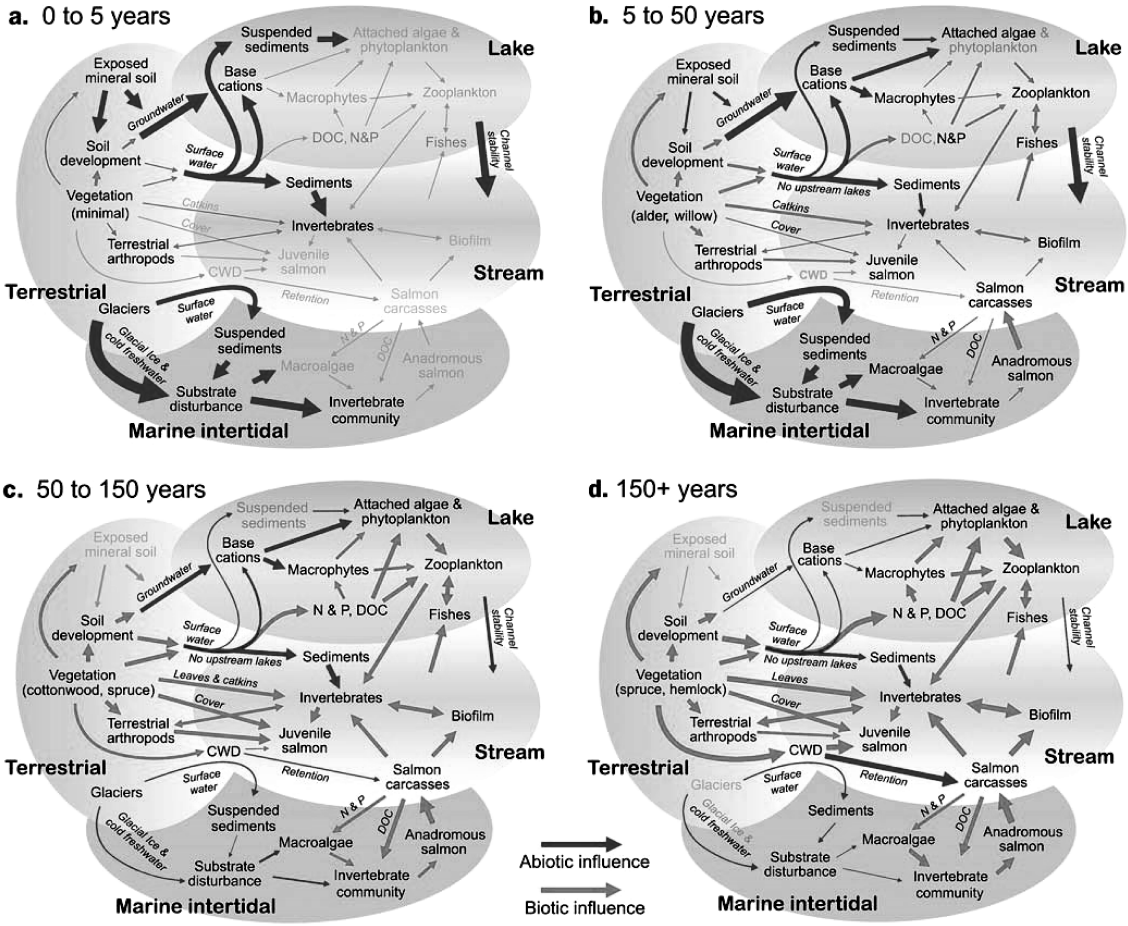

Figure 6.1: Major linkages among stream, lake, terrestrial and marine intertidal environments at Glacier Bay over four time periods (from Milner et al. 2007).

The connection with abiotic and biotic responses and feedbacks are shown here to be controlled by the initial PHT. The interconnectedness of the PHT will be shown by development from under the ice, and combined in a table which describes the roles of the major linkages proposed by Milner et al. (2007). The interconnectedness within the PHT is illustrated with a Fruchter-Reingold correlation network created in R v.3.1.2 (GUI 1.65).

6.1.1 Glacial retreat and watershed development

The glacial retreat created a salinity gradient which was lower in the fjord close to the stream estuaries of younger streams, due to more freshwater runoff. The salinity gradient controlled the presence of sea lice in juvenile salmonid diets (Chapter 5). This could affect juvenile salmonid behavior and life history; more juveniles could be using the estuaries in younger streams, and possibly increase their size and winter survival. Juvenile coho salmon were observed in tidal pools close to the streams in Wolf Point Creek (WPC) and Ice Valley Stream (IVS). No tidal pools were present around Stonefly Creek (SFC), but juvenile coho salmon were captured in the estuary in 2004. These findings elucidate the difference in salinity as a control for sea lice, and could be used as an example of salinity variability in population control and energy flow. Salinity was found to increase with time since deglaciation (Figure 5.2) ($R^2 = 0.98$, $p = 0.0011$) leading to availability and increasing MDN contribution of sea lice for in-stream juveniles.

The creation of lakes and waterbodies during glacial retreat is affected by the geomorphology and topology. However lake influence on streams system is often lost during landscape evolution (Milner et al. 2007), and the percentage of water bodies in the watershed (Figure 6.2) gives an indication of how non-permanent water bodies disappear. If no larger lakes or waterbodies are present under, or right after, glacial retreat in the watershed, then this effect will be small. Juvenile coho salmon abundance (CPUE), mean juvenile coho salmon fork length (FL) and percent aquatic food source (AFS) utilization by juvenile coho salmon correlated positively with percentage of waterbodies in the watershed. These findings indicate that lakes and wetlands are more important for juvenile coho salmon. Milner and Gloyne-Phillips (2005) found that the lakes' buffer flow variation and downstream reaches rapidly established riparian vegetation, which could explain the connection to juvenile coho salmon.

The surface area exposed after deglaciation is then influenced by denudation, and the relief ratio of the watershed decreases with stream age (Figure 6.3). This decrease affects the length of overland flow (the distance of water runoff before reaching a definite stream channel) which correlated with increasing watershed slopes (Figure 6.4). The direction and speed of watershed succession relates to the geomorphology and topology. The total number of streams in the watershed increased with stream age (Figure 6.5), due to creation of topsoil and vegetation. The weathering, vegetation littering and biotic community helps developing the topsoil with time.

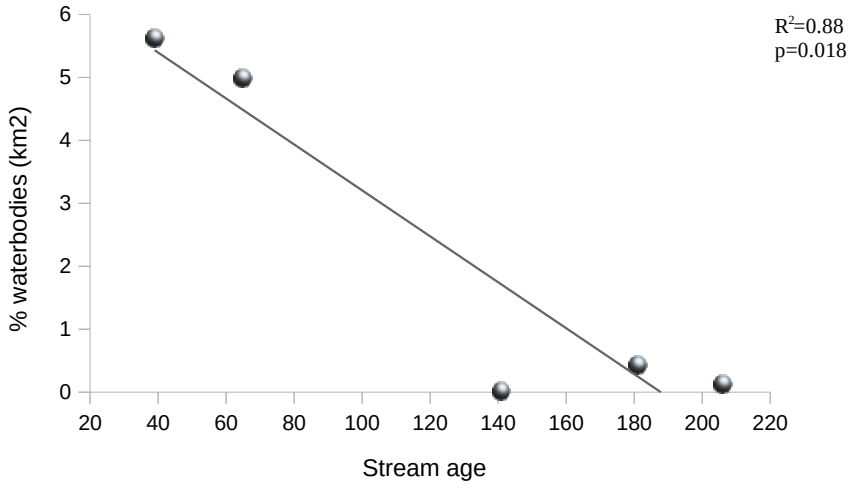

Figure 6.2: % waterbodies with stream age.

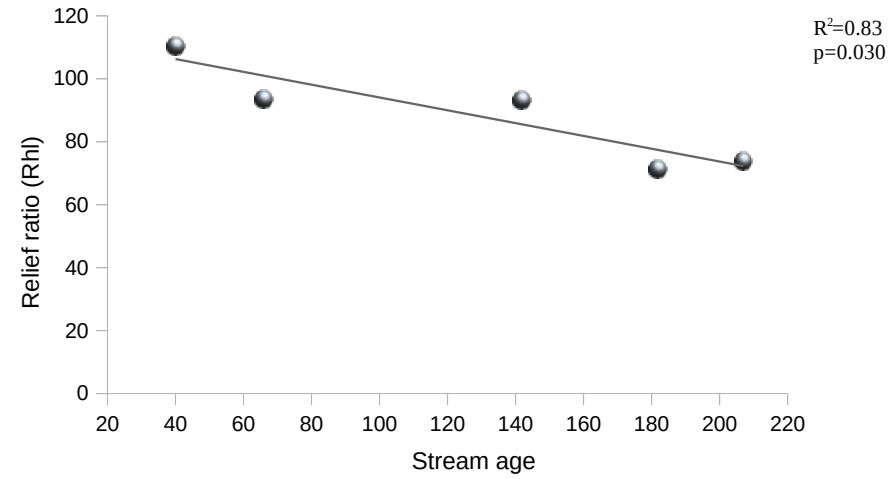

Figure 6.3: The relationship between relief ratio and stream age.

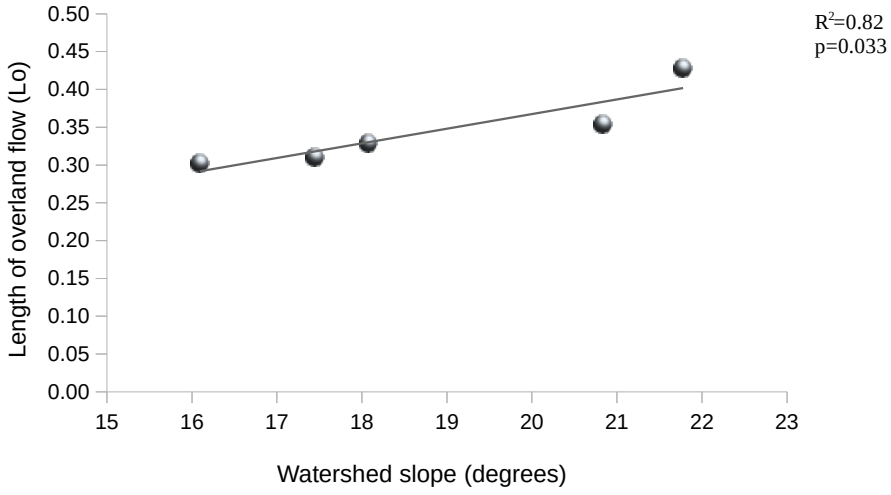

Figure 6.4: The relationship between length of overland flow and watershed slope.

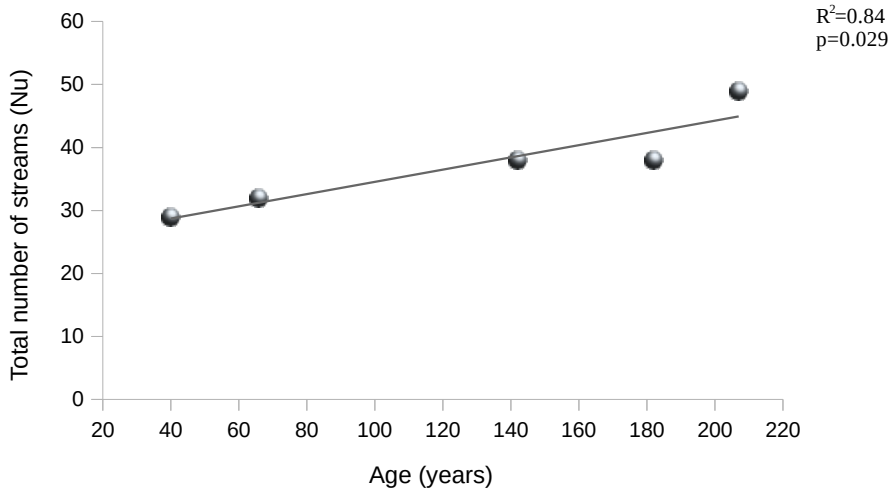

Figure 6.5: The relationship between watershed age and total number of streams.

6.1.2 Vegetation in the watersheds and terrestrial invertebrates

Milner et al. (2007) found change in the terrestrial system on a larger scale is principal driven by biotic processes. While change is influenced from feedback from biotic processes, the effect of the process seems directly controlled by the geomorphology and topology of the watershed. Percentage of vegetation cover is influenced by topology and correlated negatively with elevation, relief, ruggedness and slopes, except for main channel slope. The main channel slope only shows a low correlation, which generally would be the lowest location in the watershed. Percent vegetation cover correlated positively with elevation < 50m km^2. Percentage of watershed vegetation decreased with an increase in relief (Figure 6.6). The length of overland flow decreases with an increase in vegetation (Figure 6.7). All of these variations and changes are mainly a result of topology. Drainage density (Dd) correlates positively with elongation ratio, circularity ratio, form factor, fitness ratio and main channel slope. Dd correlates negatively with relief area, length area relation, main channel difference, compactness, watershed slope, watershed elevation and mean watershed slope, which

generally is higher in younger watersheds. An increase in vegetation cover increases the amount of dispersion of %N in stream biota (Figure 6.8), due to increased nitrogen sources that potentially could influence the contribution and availability to the stream biota. Headwaters are partially characterized by large volumes of organic matter and invertebrate input from the riparian forest, relative to steam size (Wipfli et al. 2007).

The influence of terrestrial food sources (TFS) in the diet of juvenile salmonids was studied, and the findings indicate that main channel sinuosity increased the utilization of TFS for juvenile coho salmon, which is a typical drift feeder (Nakano and Kaeriyama 1995), likely due to an increased surface area of the stream (Figure 6.9). Headwater streams make up a large portion of total stream length and watershed area (Wipfli et al. 2007), and Wipfli and Gregovich (2002) illustrated that headwaters are a source of AFS and TFS, linking upper parts of the watershed with its lower catchment. Differences in utilization of the stream by juvenile coho salmon and Dolly Varden based on diet information could be indicated by the GIS data, and could be a helpful tool in estimating population cover and competition. Only juvenile Dolly Varden correlated positively with the amount of first order streams (km^2) and percentage AFS utilization, and correlated negatively for percentage TFS utilization. This could be due to the fact that juvenile Dolly Varden utilize a negligible amount of TFS, and have larger amounts of Simuliidae in their diet, possibly indicating that juvenile Dolly Varden utilize smaller tributaries and regions higher up in the watershed compared to juvenile coho salmon, as they often were the only juvenile observed in small tributaries when using a dip net.

The stream network develops with time since deglaciation, and the number of streams in the watershed was the most clear sign of watershed development (Figure 6.5). Where stream frequency increase the amount of nitrogen increase in the stream biota (Figure 6.10), where more streams per area (km^2) supported more nitrogen in the stream biota.

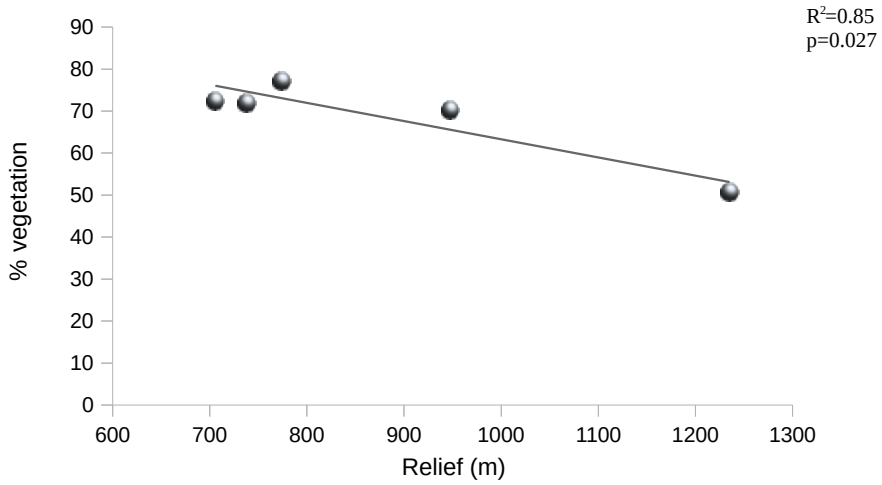

Figure 6.6: The relationship between percent vegetation cover and watershed relief.

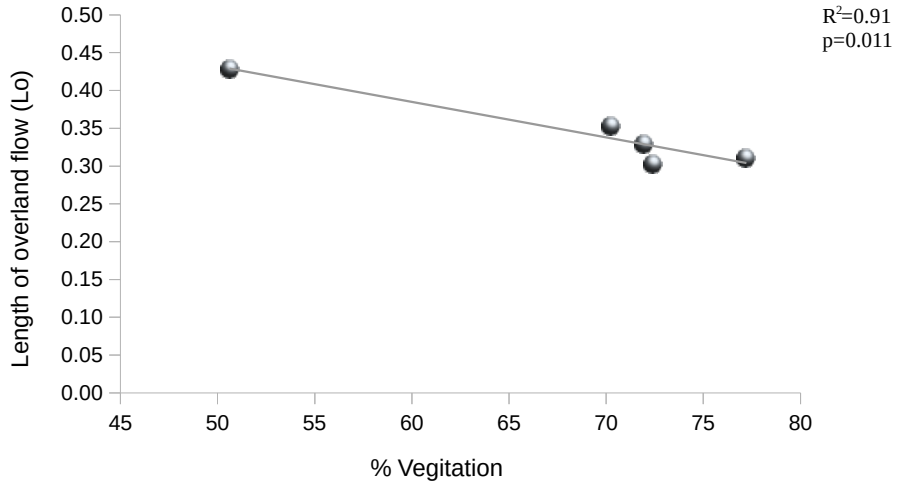

Figure 6.7: Relationship between length of overland flow and percentage of vegetation cover.

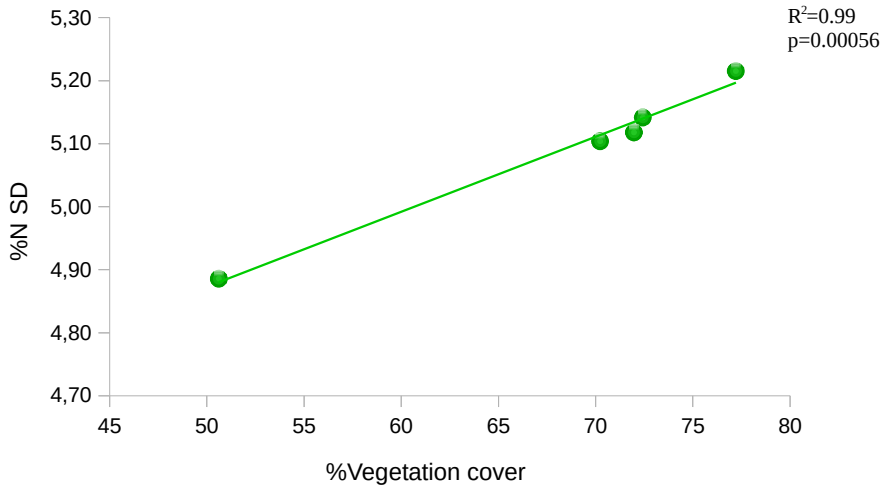

Figure 6.8: %N SD and percent vegetation cover.

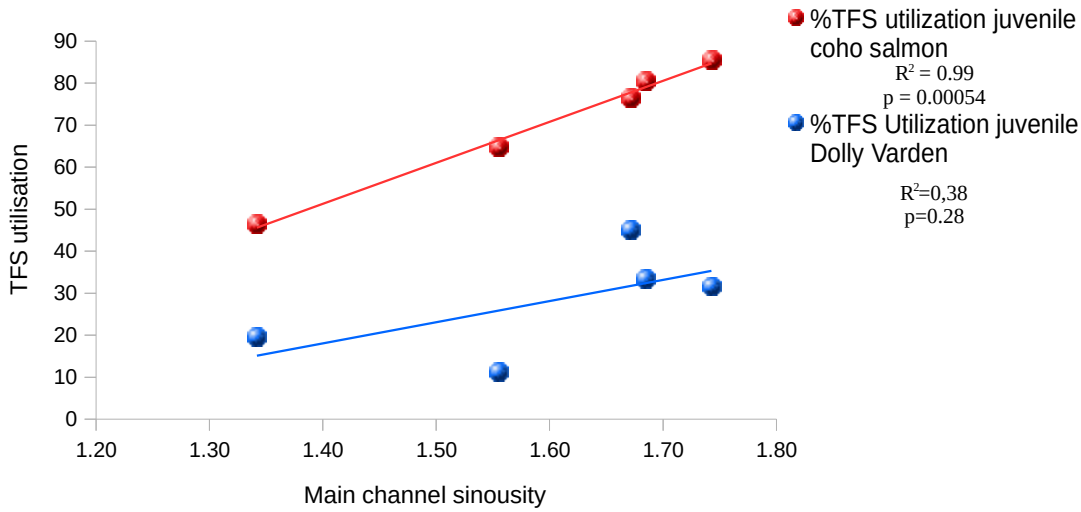

Figure 6.9: Main channel sinuosity in relation to TFS utilization (2009-2011).

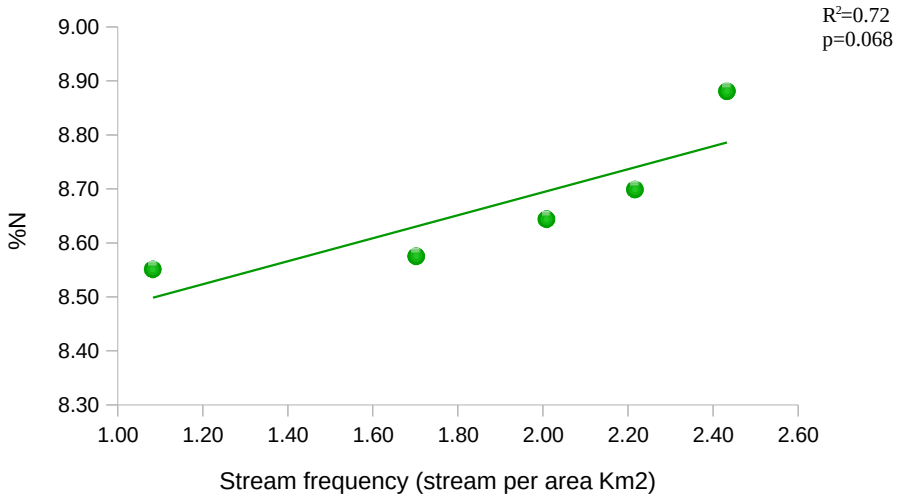

Figure 6.10: Stream frequency and %N.

6.1.3 Stream influence on nutrients, biofilm and juvenile salmonid growth

Landscape variables, such as habitat perimeter to area ratio, permeability, boundaries and relative production of tropically connected habitats affect the degree and importance of spatial subsidization (Polis et al. 1997). Climate conditions affect water levels in smaller tributaries, and wetter years may retain surface flow year-round, allowing improved summer survival and higher juvenile salmonid densities prior to overwintering (Ebersole et al. 2006). Watershed drainage time (Rho) influenced the juveniles foraging in the stream (Chapter 3). The increase in niche breadth and lower growth are linked to prolonged higher flows may be a result of flushing out of nutrients, thereby increasing the range of %N and %C found (Figure 6.11). Increase in mean bifurcation ratio is likely to lower the discharge rate and were found to decrease the range of %N and %C (Figure 6.12). This affects the biofilm %N and %C which were negatively associated with stream Rho (Figure 6.13), while biofilm %N and %C increased at higher mean bifurcation ratios (Figure 6.14). The prolonged higher flows explain why IVS and Berg Bay South Stream (BBS) have the most observed channel migration, and why juvenile coho in these streams showed lower mean FL. These results are not as clear for

juvenile Dolly Varden as for juvenile coho salmon, most likely due to different life histories. Prey resource may be depressed in IVS and BBS due to more unstable stream channels and water level variations (stream storage and discharge rate), and were therefore the two streams with the lowest diet overlap. The spatial and temporal complexity of the PHT influences nutrient contribution and availability in stream ecosystems. These results show a connection from stream geomorphology to nutrient variability in the stream environment which influences the diet of juvenile salmonids. Ecological stoichiometry handles mass balance of multiple key elements in ecological systems [e.g. carbon and nitrogen] (Cross et al. 2005), and (Junker and Cross 2014) highlighted the critical roles of both resource quality and the environmental template in regulating the importance of subsidies. Findings here suggest the PHT to be more important than resource quality, possibly due to a more stressed stream environment. (El-Sabaawi et al. 2012) found the strongest predictor of elemental C and N composition and stoichiometric ratios to be the stream where the samples were collected. The watershed PHT variables are here found to support this, as the nutrient contribution and variability seem to be a result of the PHT.

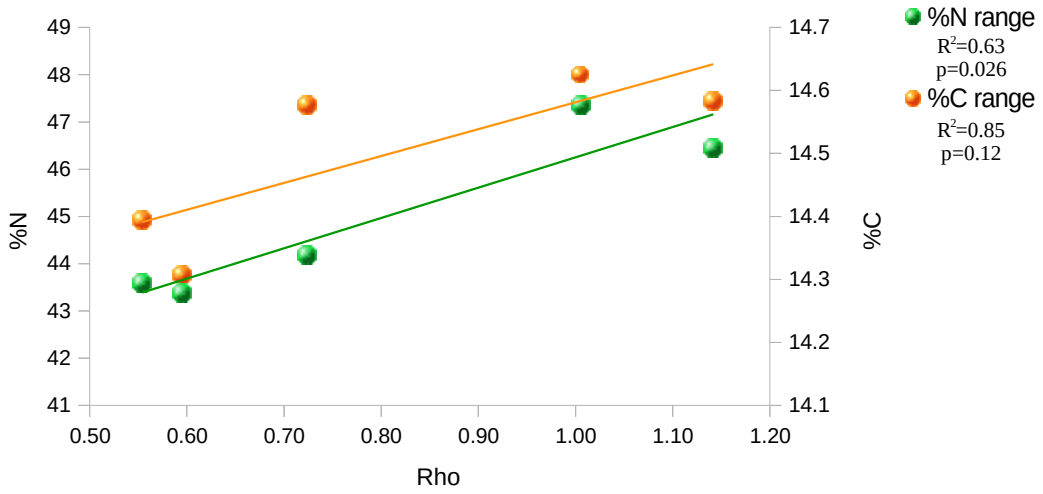

Figure 6.11: Mean bifurcation ratio influence on %N and %C range.

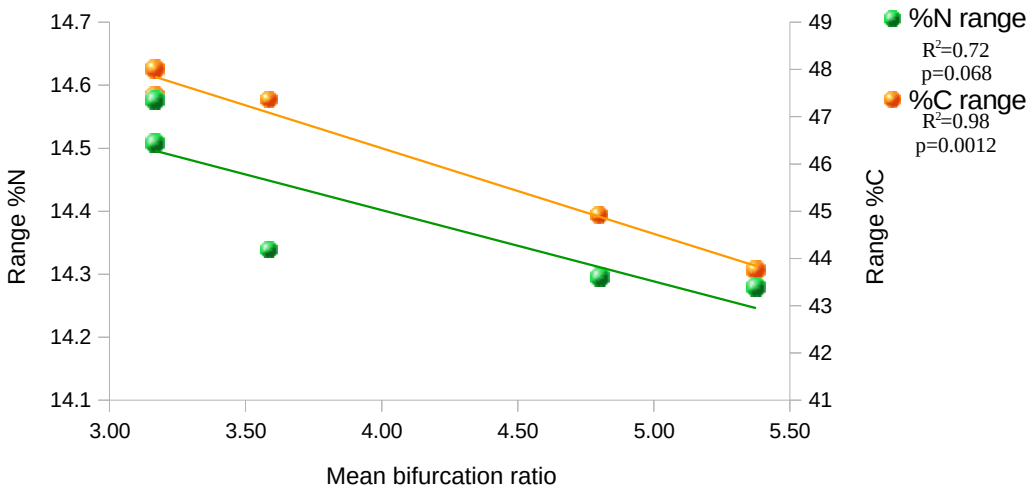

Figure 6.12: Mean bifurcation ratio influence on %C and %N range.

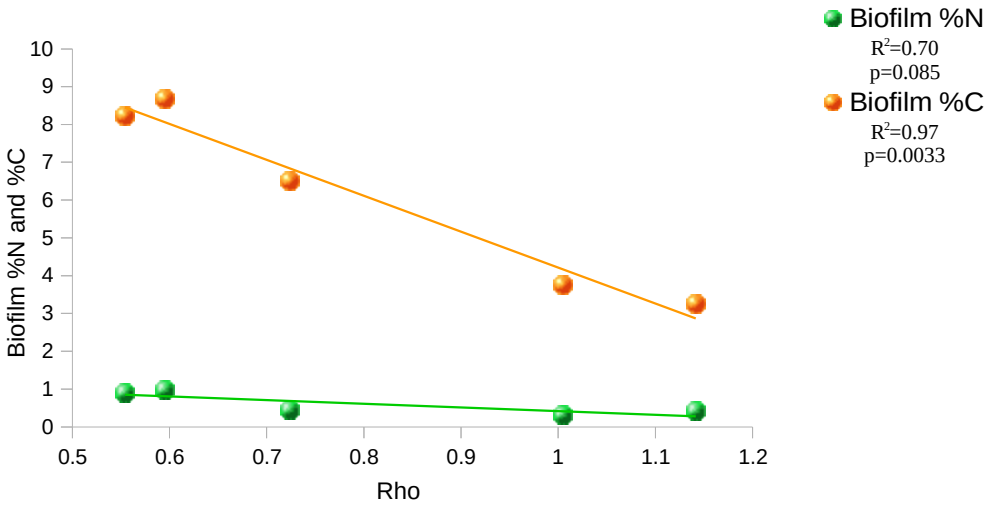

Figure 6.13: Streams Rho and biofilm %N and %C.

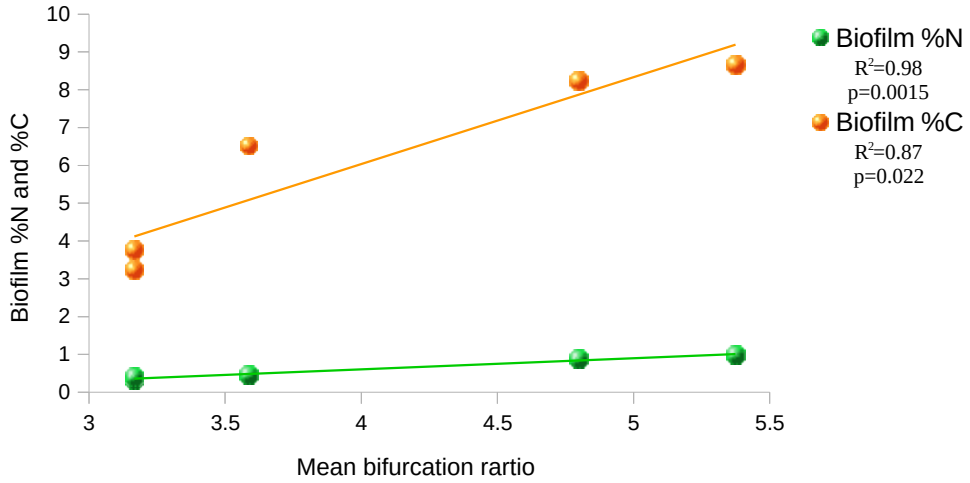

Figure 6.14: Streams mean bifurcation ratio and biofilm %N and %C.

Juvenile coho salmon and Dolly Varden dietary overlap was found in all streams except for BBS, and length and abundance increased with overlap for both species, except for juvenile Dolly Varden in IVS. The lowest overlap were found in IVS and BBS, due to higher Rho and observed channel migration influencing AFS utilization negatively (Figure 6.15), restraining growth (Figure 6.16) and decrease the diet overlap (6.17). The amount of AFS significantly influence growth of juvenile coho salmon (Chapter 3 figure 3.7).

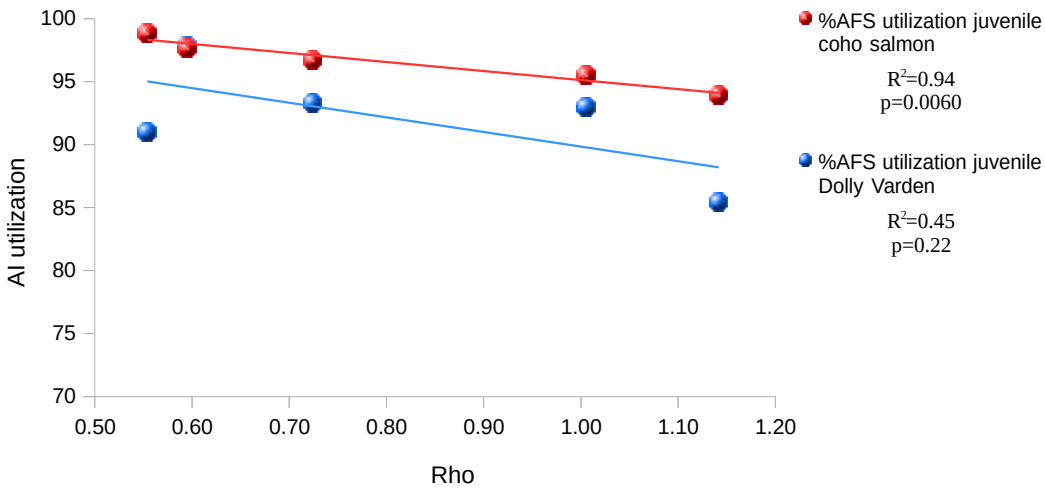

Figure 6.15: Mean Rho in relation to AFS utilization (2009-2011).

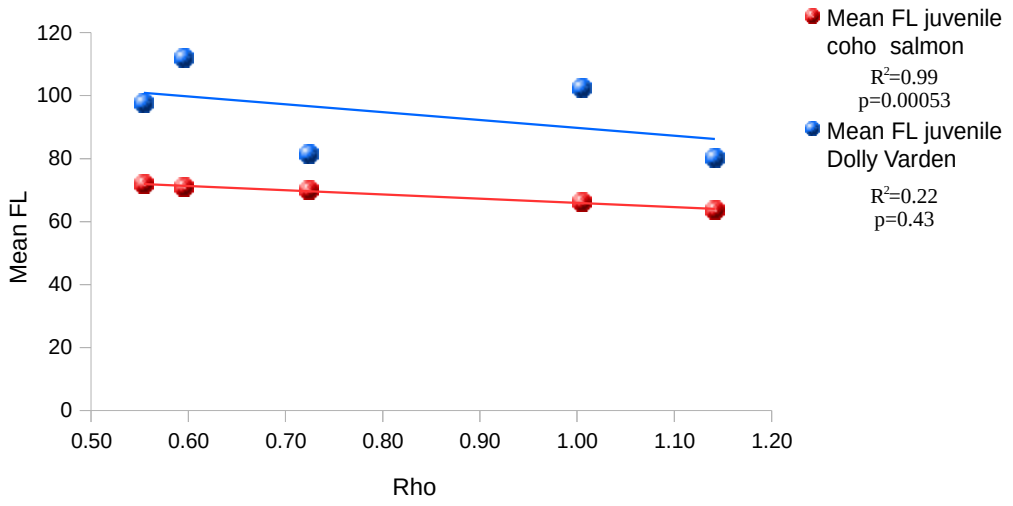

Figure 6.16: Mean Rho relation to mean FL (2009-2011).

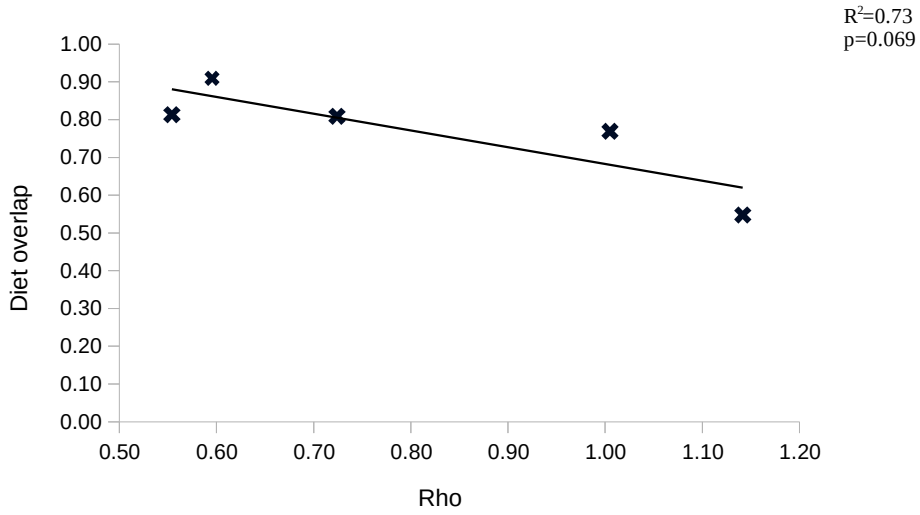

Figure 6.17: Rho in relation to diet overlap.

6.1.4 Watershed geomorphology and salmonid abundance

Constraints on fish production have traditionally been related to physical characteristics of riverine habitats like coarse woody debris (CWD), pool geometry, abundance, riparian vegetation cover and surface flow condition (Wipfli and Baxter 2010). These constraints are mostly related to stream reach scales and not on the scale of the entire watershed. The entire watershed influences the reach scale and can be responsible for many (or most) of the habitats found on a reach scale. Ziemer (1973) used geomorphology to produce an index for pink salmon production, and Swanston et al. (1977) used a quantitative approach to predict pink and chum salmon productivity. This can be taken one step further with the use of the watershed PHT, and can help produce more accurate predictions for stream productivity. The increasing quality of remotely sensing data would greatly increase the accuracy in predicting salmonid populations. Results show that relative abundance (CPUE) of juvenile coho salmon and Dolly Varden correlated with areas (km^2) < 50 m (Figure 6.18). The sampling reach was < 50 m, and provides more information in regard to this area, while also contributing bias due to

possible salmon utilization in areas > 50 m. These data indicated that rugged and steeper areas are unsuitable habitats for these species, particularly juvenile coho salmon.

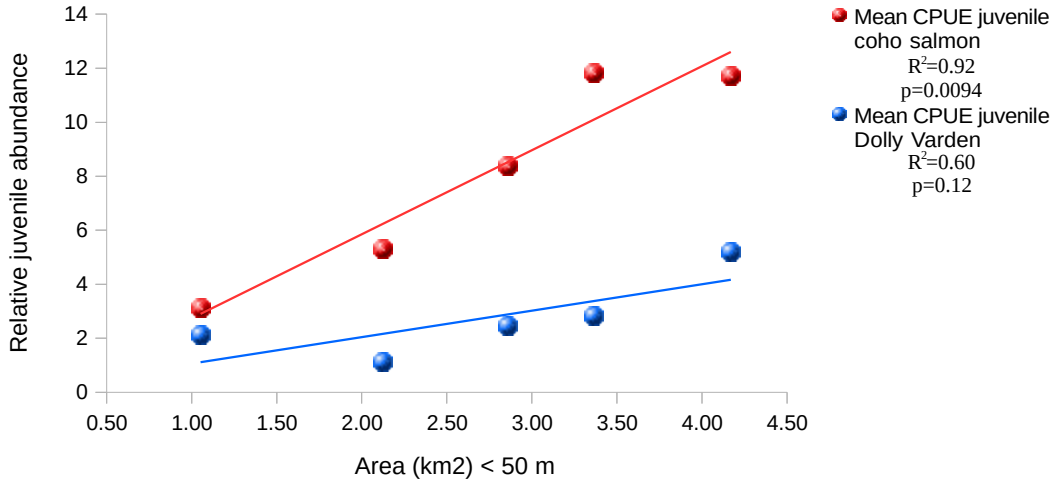

Figure 6.18: Area (km^2) < 50 m in elevation vs relative abundance of juvenile coho salmon and Dolly Varden.

6.1.5 Anadromous salmon

Results show that initial geomorphology after deglaciation affects the different watersheds in their colonization and succession of biota. The salmon colonization and contribution of MDN was linked to the abundance of spawners, the morphology of the watersheds and the accumulation of MDN over time. Verspoor et al. (2011) suggests that MDN from previous years helps supporting greater abundance of some invertebrate taxa. Rinella et al. (2011) found higher levels of $\delta^{15}N$ in juvenile coho salmon and Dolly Varden in samples from the spring compared to from fall. Stream age will affect the contribution of MDN to watersheds in different ways. Firstly by salmonids colonizing the streams resulting in MDN contribution. Rapid colonization of SFC, which both supported pink salmon and Dolly Varden within 10 years of stream formation (Milner et al. 2011), could also contribute to a faster succession due to contribution of marine nutrients. (2) Salmonid spawner abundance and the accumulation of

MDN with time itself. (3) The creation of stream retention properties due to watershed succession and increased complexity. The deglaciation of the different areas presents a wide range of geology and topology, which are major directional cues for succession. The further away from the spawner areas, the less the influence, and in many cases no impact at all. In 2004 a juvenile coho salmon (1+) found in a kettle lake, which was a spawning ground for sockeye salmon, had a $\delta^{15}N$ value as high as 12.95‰ (earlier findings). The relation between mean $\delta^{15}N$ and mean total MFS (2009-2011) for juvenile coho salmon and Dolly Varden (Figure 6.19) shows the strong connection between watershed $\delta^{15}N$ and MFS in the salmonid diet. Percentage of MFS utilization by juvenile coho salmon and Dolly Varden, pink salmon spawner abundance and $\delta^{15}N$ levels all correlated positively with watershed area (km^2) and total stream length. Mean $\delta^{13}C$ and mean FL length of juvenile Dolly Varden correlated positively with main channel elevation differences. Pink salmon spawner abundance seems more important to juvenile Dolly Varden compared to juvenile coho salmon. Robustness of $\delta^{15}N$ patterns on a small or large scale within and among ecosystems, across taxa and lifeforms (Robinson 2001) can be used with GIS to assess the retention and contribution of MDN to the different areas of the watershed. Reimchen et al. (2002) demonstrated a direct link between salmon spawning densities and $\delta^{15}N$ in humus soil, riparian vegetation and riparian insects. This will help us understand the spatial spread of salmonid populations across a watershed. Pink salmon spawner abundance correlates positively with the size of the watersheds and stream systems, and suggests that watershed size and length support higher pink salmon populations. PHT variables are then linked to juvenile salmon abundance and growth and show the interconnectedness of the PHT. Marczak et al. (2007) found consumer density or biomass changes in response to subsidies to be inconsistent across habitats, trophic and functional groups. While subsidies can be substantial, the questions if and how they will be utilized still remain unclear.

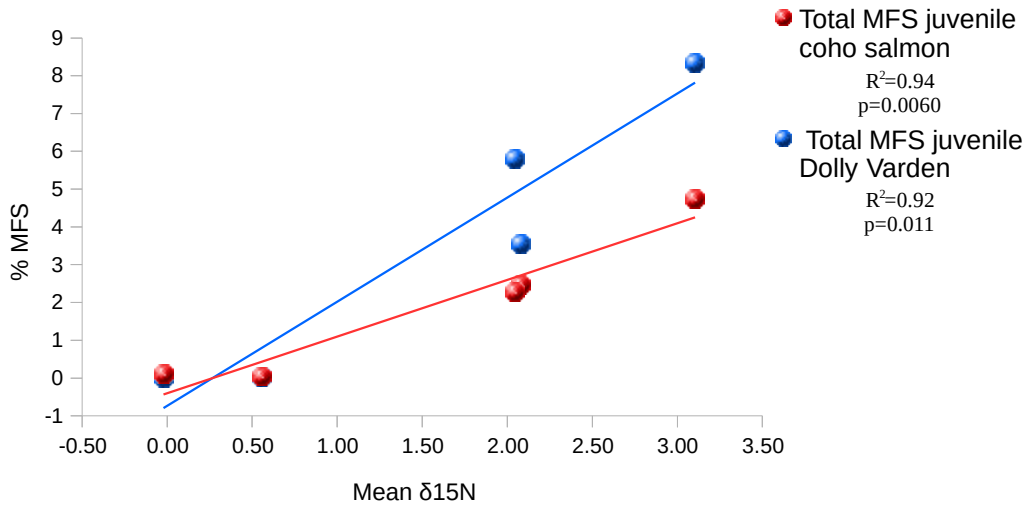

Figure 6.19: Mean total MFS in the diet (2009-2011) against mean d15N (2011).

6.1.6 Interconnectedness at a watershed scale

All landforms are a function of structure, process and time (Davis 1899). Glacier Bay National Park is unique due to the short temporal scale (< 250 years) from lower to upper bay regions, giving rise to the opportunity to study the colonization and development of watersheds after deglaciation. Landscape evolution is influenced by several factors, and chaos (deterministic complexity) may be the key to developing a theory of landscape evolution reconciling presence of random, irregular variability and orderly regular patterns (Phillips 1993). The exchange and reuse of energy and material at the earth's surface through complex interplay of biological, geological and chemical processes (Hedges 1992) are hard to understand and predict. Larger and spatial differences can be identified and assessed with help of remote sensing and GIS. This gives us a better understanding of watershed ecosystems and cross-boundaries effects of nutrient flow and animal migration. Connectivity among systems varies enormously, from near total isolation to strong mixing (Polis et al. 1997). Salmonid contributions of MDN following spawning to natal streams enhance succession and colonization of other groups, and in turn transports MDN across environments, from aquatic

to semi-aquatic and terrestrial. The effect of spawning salmonids will therefore influence the in-stream juvenile fish, both when spawning and nutrient leaching from retained carcasses and MDN nutrient pools. These data correspond with reciprocal subsidies dynamic of terrestrial and aquatic food webs (Nakano and Murakami 2001) and can help us understand how geomorphology and topography influence the contribution and distribution of cross-boundary subsidies on the food webs, based on the watershed PHT.

Topography and topology can be particularly important for spatial patterns of water fluxes and dissolved matter in catchments with shallow soils (Jencso et al. 2010). Topology and relief is found in the correlation network to be a strongly influencing factor in how the watershed develops over time (Figure 6.20). Milner et al. (2007) found stream ecosystems to be unique compared to terrestrial, lake and marine intertidal ecosystems, remaining more strongly dominated by physical processes, with a general increase in the influence of biotic processes with ecosystem development. These findings indicate the connections between geomorphology and vegetation development, which are rarely taken into account. The dependency of scale in ecosystems could be continuous, causing every change in scale to bring changes in patterns and processes (Wiens 1989). Even though cross boundary nutrient transfer is receiving greater attention these days, the reason for changes and variation of these nutrient fluxes on a watershed scale is almost non-existent. The use of GIS, geomorphology and hydrology on a watershed scale will greatly increase the understanding of nutrient transfer, migration patterns and population interactions of Pacific salmon and stream invertebrates. Milner et al. (2011) found macroinvertebrate community assembly to initially appear strongly deterministic, while that of microcrustacean was more stochastic. A network of correlations shows the interconnectedness between geomorphology, juvenile abundance, diet and spawner effects. Although this study only covered five streams, the results indicate connections and provide a basis for further research and testing. This can help to explain the deterministic or stochastic effects in a watershed, and that nonlinear chaos drives the casualty in space and time.

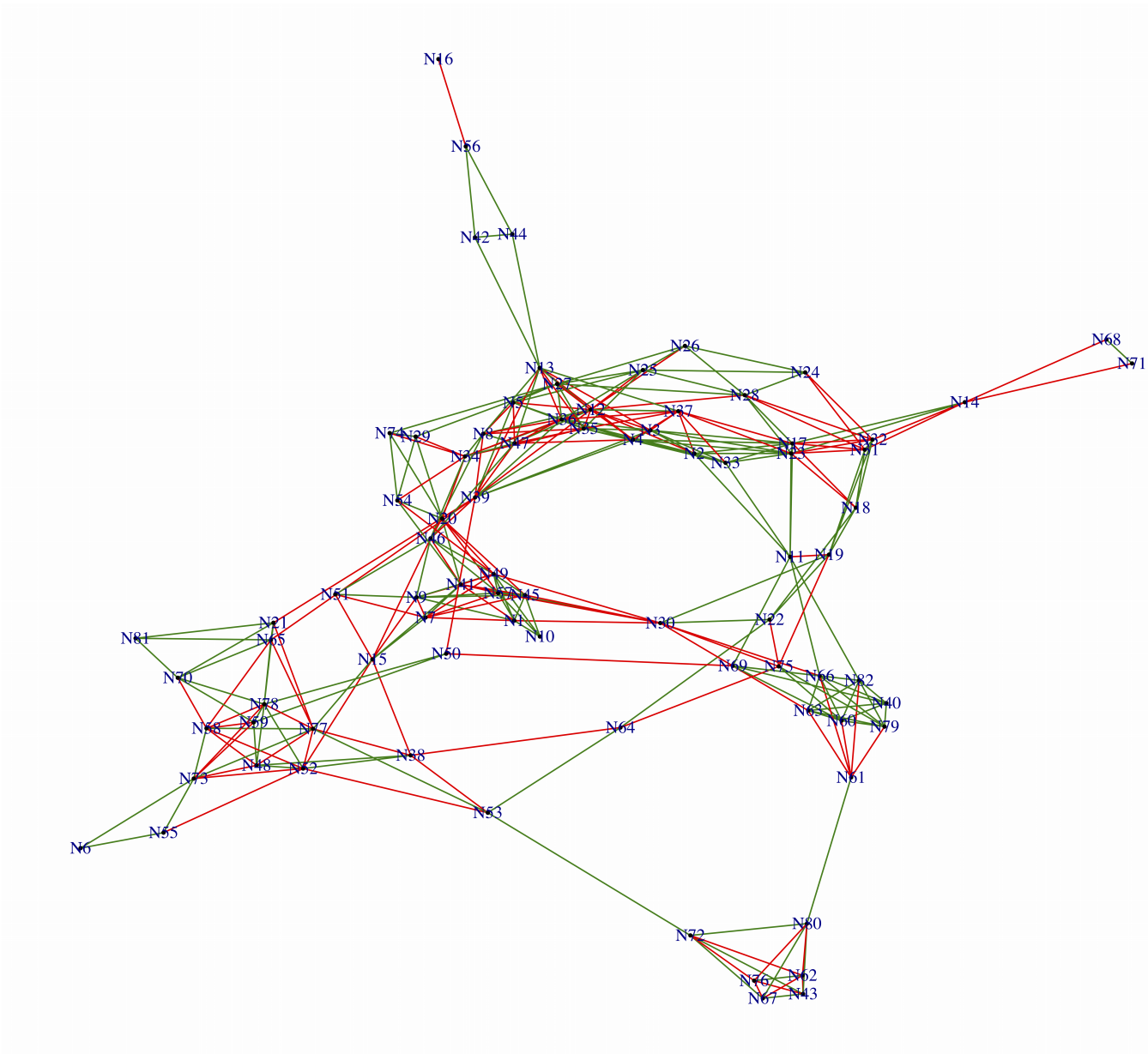

Figure 6.20: Correlation network (CC < 0.85) showing the interconnectedness within the watershed PHT. Key found in Appendix 3.

Morphology, climate and location influence and control development of the watershed. The space-time continuum of landscapes are controlled by deterministic chaos (deterministic complexity) due to the physical habitat template present at a specific point in time, as a past and present biosphere do not exist independently (Rull 2014). The physical habitat template is continuously influenced by the presence of "noise" in form of stochastic influence. Glacier Bay study streams are shown, with the use of GIS, to be an *in-situ* laboratory for studying changes with time, and how the initial PHT controls vegetation, stream development and biotic factors. There is a perceptual bias imposed by the observer, since every organism is an "observer" of the environment (Levin 1992). The PHT can be of use in this respect due to the fourth dimension, time, in a four dimensional space (x,y,z,t), as the change of the three dimensional space form point t_1 to t_2 could be centered around one organism in the watershed. Ecological organization is a result of space and time.

The major linkages proposed by Milner et al. (2007) have been shown with the PHT analysis to be nonlinear, and the change is normally a combination of different variables varying both spatially and temporally. Stream network creation and watershed denudation seem to be the most linear effects found among the streams, and a more continuous effect compared to vegetation cover. The initial PHT is controlling the effect and how strong the feedback from the biotic variables is over time, which again influences ecological stoichiometry. Findings demonstrate a nonlinear system where the abiotic physical habitat controls the colonization and succession of biotic communities and their level of feedback to the PHT. To improve this model the physical habitat and the causality from the initial PHT after glacial retreat needs to be addressed. Within stream productivity is a result of channel storage per unit area (Rho) and the stream discharge rate (Bifurcation ratio). Cross boundary subsidies are a result of the PHT, which controls contribution and retention between terrestrial, lake, stream and marine intertidal. Salmon spawners contribute MDN, but the PHT influences retention and nutrient availability.

Table 6.1: Table summarizing the nonlinearity of the major linkages between ecosystems over time (cf Milner et al. 2007).

Environment	Watershed development (PHT)	Effect
Glacial	Role of glaciers	Glacial ice and cold fresh water influence decreases with stream age, creating an increasing salinity gradient in the fjord outside young to older streams after glacial retreat (see chapter 5, Figure 5.2).
Lake	Role of lake	Lakes develop after glacial retreat due to geomorphology and topology, created by glacial erosion, sediment depositions, and remnant ice. Several lakes and water-masses disappear after glacial retreat (see Figure 6.2). Topology and geomorphology set the condition for lake existence.
Terrestrial	Role of exposed ground	Exposed ground increases with glacier retreat, and decreases with age due to soil and vegetation development, but is influenced by the topology and geomorphology in how fast and how much soil and vegetation cover expand. Where increasing slope increases the length of overland flow (see figure 6.4).
	Role of soil	Soils increases with weathering of exposed ground, fluvial deposits, and vegetation development, creating feedbacks through litter-fall and organic deposits. Water surface flow increases with soil development, while decreases with the development of stream network. Topology and geomorphology still influence the effect, as the length of overland flow increases with mean watershed slope (see Figure 6.4), and number of streams increase with age as a result of creation of soil and vegetation (see Figure 6.5). And length of overland flow decreases with percentage of vegetation cover (see Figure 6.6), which is impacted by the relief (see Figure 6.7).
	Role of vegetation	Vegetation increases with watershed age, but distribution and percentage of vegetation cover are controlled by topography and geomorphology (see Figure 6.7). Vegetation influences soil and stream network development, and lessens the amount of infiltration to groundwater and increases surface runoff (see Figure 6.6). Increasing vegetation also increases the colonization and succession of terrestrial invertebrates. Increased vegetation cover shows increased variation in stream %N biota (see Figure 6.8).
	Role of CWD	CWD is controlled by geomorphology and topology, but large woody debris (LWD) increases with age due to larger vegetation.
	Role of terrestrial invertebrates	An increase in terrestrial invertebrates, which increase their contribution to lake, stream and marine intertidal environments. The contribution of terrestrial invertebrates found in the in-stream juvenile salmonid diet were controlled by main stream sinuosity (see Figure 6.9), creating a larger stream surface area.
Stream	Role of stream network	Stream network, or the number of streams increase with age, and are the best indicator of linear distribution next to salinity with stream age (see figure 6.5). More streams per area supports more %N (see figure 6.10), and could help us in understanding nutrient transfer.
	Role of stream sediments	Stream suspended sediments will decrease with time since glacial retreat and will wash out and settle into lakes or the marine inertial environment.
	Role of N and C	Carbon and nitrogen increase after glacial retreat, but the distribution is controlled by watershed PHT. Carbon and nitrogen of the stream biota were indicated to be influenced by stream Rho and mean bifurcation ratio (see Figure 6.11 and 6.12), where the range of N and C in biota increased with Rho, and decreased with mean bifurcation ratio.
	Role of stream biofilm	Biofilm is important in several processes, and the %C and %N in biofilm are influenced by stream Rho and mean bifurcation ratio (see Figure 6.13 and 6.14).
	Role of stream invertebrates	Stream invertebrates is the main driver in juvenile coho and Dolly Varden growth (see chapter 3), while the stream invertebrates diet utilization by juveniles seem to be influenced by Rho (see Figure 6.15).
	Role of juvenile salmonids	Juvenile salmonids increase with time since colonization and transport nutrient from the stream network to the marine environment, and to terrestrial environment by predation. Juvenile salmonid abundance is related to the PHT. Area (km^2) < 50 m in elevation supported higher abundance of juvenile salmonids (see Figure 6.18).
Marine intertidal	Role of marine intertidal invertebrates	Marine intertidal invertebrates increase with deglaciation, and the salinity increases influence the biota present from young to older streams.
	Role of anadromous salmon	Anadromous salmonids contribute MDN to stream, lake and terrestrial environments, and a direct food source for juvenile fish (see figure 6.19). This cross environment MDN transfer by salmon spawners are seen in stream biota in the study streams. Further transport by predators and emerging stream invertebrates and semi-aquatic invertebrates for instance spiders.

6.2 Limitations

These data presents the connections within watersheds as a function of space and time, but limitations occur in that only five streams were studied and more replications may be necessary.

The isotopic sampling was only done once in early fall, and does not provide an overall picture of salmon spawner contribution of MDN. While pink salmon were the most abundant spawner in these streams, there are also other species that will contribute to the system.

Minnow-trapping were only done in one reach of the stream, and contribution to the knowledge of habitat distribution and watershed utilization is therefore limited. Trapping were only undertaken one time during the year, limiting the understanding of watershed migration and utilization.

The five study streams only provide five variables. This is not enough to test predictive features based on the model presented.

6.3 Future research

Understanding the development of watersheds over time will contribute to the knowledge and the practical uses this provides. Relationships between morphological features of the watershed and the in-stream juvenile salmonid abundance, growth, diet overlap and niche breadth can explain the juvenile salmonids in-stream utilization of habitats and population processes. The temporal changes can more readily be identified by analyzing and

understanding the differences on a spatial scale. The estimations and predictions on accumulation and loss of nutrients, salmon population estimation and prediction of carrying capacity will be of great use, both from a research-, government- and a resource management point of view. Movement of nutrients, detritus, prey and consumers can be studied at a spatial scale with the use of newer and more accurate remote sensing equipment/tools, and will help us understand the changing processes on a watershed scale. This approach can also aid us in understanding the overall structure and interactions of abiotic and biotic factors over time, as well as biodiversity assessments.

The findings show that the watershed PHT influences nutrient variability, and will need further examination, as this limits the understanding of retention of MDN in the watershed. In order to be able to model population dynamics and MDN contribution, future research should include nutrient transport on a watershed scale, isotope sampling and salmonid spawning abundance. The modeling of bearing capacity with the help of GIS could lead to the development of a management tool to assess capacities and return for fisheries and department work. Correlation and principal component analysis (PCA) suggests succession with time, but the "initial" state of the watershed after deglaciation influences the temporal and spatial scale of development, and may enhance colonization. Isotope sampling and minnow trapping were only performed at a reach in the lower area of the main channel and thus future studies should include several sites throughout the watershed so as to be able to better assess the impacts of the watershed on the salmonid production. Estimations can also be made of the scale of processes and patterns in watersheds temporally with the help of PHT. The model should be tested in different biomes and landscapes to help us understand how space and time influence processes around us. This should also be included in climatic research, and can provide information on the landscape effect on precipitation, as 3D remote sensing is available for wind and temperature, and can be included in the PHT to understand change in time. These

findings provide important information in river restorations and provide knowledge into the legacy of the riverscape, which has implications in dam removal restorations.

6.4 Concluding remarks

This thesis has improved the knowledge of interconnectedness of watershed habitats, and how the physical habitat influences the stream system and shows the chaos (deterministic complexity) behind it. This study has demonstrated that combining variables found with remote sensing GIS in addition to diet and MDN sampling undertaken on a reach scale are influenced by the PHT of the watersheds in all aspects of the stream ecosystem. The physical habitat influences the nutrient variation in the stream, which again affects the foraging and growth of juvenile salmonids. This is the first time sea lice has been found to be a part of instream juvenile fish diet, and illustrates the change of fjord salinity in controlling their contribution. The uniqueness of Glacier Bay also provides insight in the distribution of MDN, and how the PHT and MDN abundance influence discrimination $\delta^{15}N$ and $\delta^{13}C$. It is of great importance for researchers to understand how food webs and stoichiometry are influenced by the PHT.

This thesis also provides a model to help understand how the environments and habitats are influenced by each other, and provides a platform for understanding temporal change within the PHT. This model can be used in any biome, and is therefore universal.

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7. Appendices

1. Watershed geomorphology variables correlation table.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
1 Age	0.30																																						
2 Area (km²)	0.10	-0.10																																					
3 Area elevation bellow 50m (km²)	0.40	0.90	0.20																																				
4 Basin length (km) (Lb)	-0.10	-0.90	0.50	-0.70																																			
5 Circulatory Ratio (Rc)	0.10	0.90	-0.50	0.70	-1.00*																																		
6 Compactness	0.00	0.70	-0.60	0.60	-0.90	0.90																																	
7 Constant of channel maintenance	0.00	0.70	-0.60	0.60	-0.90	0.90	-1.00*																																
8 Drainage density	-0.10	-0.60	0.30	-0.70	0.70	-0.90	0.90	0.90																															
9 Elongation Ratio (Re)	0.30	0.70	0.10	0.90	-0.60	0.70	-0.70	-0.70	-0.90																														
10 First order streams length (km)	0.70	-0.20	0.50	-0.10	0.50	-0.50	0.70	0.70	0.60	-0.30																													
11 Fitness Ratio (Rf)	-0.10	-0.60	0.30	-0.70	0.70	-0.90	0.90	0.70	1.00*	-0.90	0.60																												
12 Form Factor Ratio (Rf)	-0.70	0.20	-0.50	0.10	-0.50	0.50	0.70	-0.70	-0.60	0.30	-1.00*	-0.60																											
13 Hack mean main channel elevation diff	-0.90	-0.60	-0.30	-0.70	-0.10	-0.30	-0.10	0.10	0.20	-0.50	0.60	0.20	0.60																										
14 Hack mean main channel gradient	-0.30	-0.70	-0.10	-0.90	0.60	-0.60	-0.70	0.70	-0.90	-0.70	0.30	0.90	-0.30	0.50																									
15 Hack mean main channel slope	-0.10	-0.70	0.20	1.00*	-0.70	0.70	0.90	-0.60	-0.70	0.90	-0.10	-0.70	0.10	0.10	-0.90																								
16 Hack main channel (km)	0.40	0.90	0.20	1.00*	-0.70	0.70	0.60	-0.60	-0.70	0.90	-0.10	-0.70	0.10	0.10	-0.70	0.90																							
17 Length Area Relation	0.30	1.00*	-0.10	0.90	-0.90	0.90	0.70	-0.70	-0.60	0.70	-0.20	-0.60	0.70	0.70	-0.90	0.90	0.70																						
18 Length of overland flow (Lo)	0.00	0.70	-0.60	0.60	-0.90	0.90	1.00*	-1.00*	-0.90	0.70	-0.70	-0.90	0.70	0.70	-0.90	0.70	0.70	0.60																					
19 Length ratio (LJ)	-0.10	0.60	-0.70	0.20	-0.80	0.80	0.60	-0.60	-0.90	0.00	-0.40	-0.20	0.40	0.00	0.60	0.60	0.60	0.60	0.60																				
20 Main channel azimuth	-0.90	-0.40	0.20	-0.30	0.30	-0.30	-0.10	0.10	-0.60	-0.10	-0.60	0.00	0.60	0.80	0.00	0.30	-0.40	-0.10	-0.30	-0.30																			
21 Main channel sinuosity	0.10	-0.50	0.40	-0.70	0.20	-0.20	-0.10	0.10	0.30	-0.60	0.10	0.30	-0.10	0.30	-0.70	0.60	0.40	0.90	0.50	0.30	0.30																		
22 Max watershed slope in degrees	0.10	0.40	-0.80	0.30	-0.70	0.70	0.90	-0.90	-0.80	0.50	-0.60	-0.80	0.60	0.00	-0.50	0.30	0.40	-0.10	0.20	0.50	-0.30	0.80																	
23 Mean Bifurcation ratio (Rb)	-0.56	0.21	0.56	0.36	-0.05	0.05	0.05	-0.05	-0.21	0.36	-0.41	-0.21	0.41	0.21	-0.36	0.36	0.21	0.05	-0.21	0.72	-0.87	0.80	0.21																
24 Mean watershed elevation (m)	0.10	0.60	-0.30	0.70	-0.70	0.70	0.90	-0.90	-1.00*	0.90	-0.60	-1.00*	0.60	-0.20	-0.90	0.70	0.60	1.00*	0.60	0.00	-0.30	-0.20	0.00	0.90															
25 Mean watershed slope in degrees	0.00	0.70	-0.60	0.60	-0.90	0.90	1.00*	-1.00*	-0.90	0.70	-0.70	-0.90	0.70	-0.10	-0.70	0.60	0.70	1.00*	0.60	-0.10	-0.10	0.90	0.05	0.05	0.90														
26 Median watershed elevation	0.00	0.70	-0.60	0.60	-0.90	0.90	1.00*	-1.00*	-0.90	0.70	-0.70	-0.90	0.70	-0.10	-0.70	0.60	0.70	1.00*	0.60	-0.10	-0.10	0.90	0.05	0.05	0.90	1.00*													
27 Median watershed slope Degrees	0.10	0.40	-0.80	0.30	-0.70	0.70	0.90	-0.90	-0.80	0.50	-0.60	-0.80	0.60	0.00	-0.50	0.30	0.40	0.90	0.50	-0.20	0.30	0.50	0.56	0.70	0.80	0.90	0.90											
28 Melton ruggedness number	-0.60	0.10	-0.20	0.20	-0.30	0.30	0.60	-0.60	-0.70	0.50	-0.90	-0.70	0.90	0.50	-0.50	0.20	0.10	0.60	0.00	0.70	-0.30	0.50	0.70	0.60	0.60	0.60	0.50	0.10										
29 Perimeter (km)	0.30	1.00*	-0.10	0.90	-0.70	0.70	0.90	-0.90	-1.00*	0.90	-0.60	-1.00*	0.60	-0.20	-0.90	0.70	1.00*	0.60	0.00	-0.40	-0.50	0.80	0.21	0.60	0.70	0.70	0.40	0.70	0.60									
30 Relief (m)	0.10	0.60	-0.30	0.70	-0.70	0.70	0.90	-0.90	0.00	-0.10	0.60	0.00	0.60	0.80	0.10	-0.30	0.60	0.90	0.50	0.00	-0.30	0.80	0.21	1.00*	0.90	0.90	0.80	0.70	0.00	0.00								
31 Relief Ratio (Rhl)	-0.90	-0.40	0.20	-0.30	0.30	-0.30	-0.10	0.00	0.00	-0.10	0.00	0.00	0.20	-0.20	-0.90	0.70	0.60	0.90	0.50	0.00	-0.30	-0.20	0.72	0.00	-0.10	-0.10	-0.20	0.40	0.10	0.00	-0.90							
32 Rho	0.70	0.30	-0.60	0.10	-0.40	0.40	0.30	-0.30	-0.10	0.00	-0.10	-0.30	-0.30	-0.50	0.00	0.10	0.30	0.30	0.50	-0.90	-0.30	-0.20	-0.87	0.10	0.30	0.30	0.50	0.80	0.70	0.30	0.00	-0.20						
33 Stream_Freq. (s)	0.30	-0.70	0.60	-0.40	0.90	-0.90	-0.80	0.80	0.50	-0.30	0.70	0.50	-0.70	-0.10	0.30	0.40	-0.70	0.30	0.50	-0.90	0.00	0.00	-0.15	-0.50	-0.80	-0.80	-0.60	-0.50	-0.40	-0.50	0.00	-0.90	0.29					
34 Stream order	0.87	-0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.58	0.00	0.00	-0.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.89*	0.00	0.00	0.00	0.29	-0.58	0.00	-0.50	0.00	0.87	0.00	0.89*				
35 Total number of streams (Nu)	0.97*	0.21	0.05	0.36	-0.05	0.05	0.05	-0.05	-0.21	0.36	0.62	-0.21	-0.62	-0.82	-0.36	0.36	0.21	0.05	-0.21	-0.82	0.15	0.21	-0.58	0.21	0.05	0.05	0.21	-0.46	0.21	0.21	-0.82	0.67	0.36	-0.72	0.21			
36 Total stream length (km)	0.30	1.00*	-0.10	0.90	-0.90	0.90	0.70	-0.70	-0.60	0.70	-0.20	-0.60	0.20	-0.60	-0.70	0.90	1.00*	0.60	0.00	-0.40	-0.50	0.80	0.21	0.60	0.70	0.70	0.40	0.70	0.60	0.60	-0.40	0.30	-0.70	0.00	0.21			
37 Waterbodies (km²)	-0.60	0.40	0.30	0.30	-0.30	0.30	-0.10	0.00	0.00	0.10	-0.40	0.00	0.40	0.20	-0.30	0.30	0.40	0.00	0.30	0.30	-0.50	0.80	0.21	0.00	0.10	0.10	0.40	0.10	0.40	0.00	0.50	-0.60	-0.50	-0.87	-0.50	0.40		
38 % Vegetation in the watershed	0.40	-0.50	0.70	-0.30	0.80	-0.80	-0.90	0.90	0.70	-0.40	0.90	0.40	-0.90	-0.60	0.40	-0.10	-0.50	-0.90	-0.30	-0.20	-0.50	-0.60	-0.15	-0.70	-0.90	-0.90	-0.80	-0.70	-0.50	-0.70	-0.20	-0.10	0.90	0.29	0.36	-0.50	0.90	
39 % Waterbodies in the watershed	-0.70	0.00	0.40	-0.10	0.10	-0.10	-0.30	0.30	0.40	-0.30	0.40	0.40	0.20	0.40	0.30	-0.10	0.00	0.60	0.10	0.60	-0.50	-0.60	0.72	-0.40	-0.30	-0.30	-0.60	0.10	0.00	-0.40	0.60	-0.70	-0.20	-0.87	-0.82	0.00	0.90	0.00

2. Combined groups and excluded items.

	Prey items >10% of total diet		
Combined groups:	Chironomidae excuvia	Chironomidae larvae exuviae	
		Chironomidae pupa exuviae	
	Simuliidae excuvia	Simuliidae larvae exuviae	
		Simuliidae pupa exuviae	
	Other diptera larvae	Empididae larvae	**Grouped into Other Diptera**
		Tipulidae larvae	
		Sciomyzidae larvae	
		Blephariceridae larvae	
		Canacidae larvae	
		Dixidae larvae	
		Muscidae larvae	
		Ephydridae larvae	
		Unidentified Diptera larvae	
		Ceratopogonidae larvae	
	Other diptera pupa	Ceratopogonidae pupae	
		Empididae pupae	
		Tipulidae pupae	
		Blephariceridae pupae	
		Dixidae pupae	
		Unidentified Diptera pupae	
	Other diptera exuviae	Ceratopogonidae pupae exuviae	
		Unidentified Diptera larvae exuviae	
		Unidentified Diptera pupae exuviae	
	Other diptera adult	Ceratopogonidae adult	
		Tipulidae adult	
		Sciomyzidae adult	
		Phoridae adult	
		Unidentified Diptera adult	
	Crustacea	Cladocera	
		Copepoda	
		Amphipoda	
		Ostracoda	
	Other AFS	Juvenile salmonids	
		Plecoptera exuviae	
		Trichoptera pupae	
		Trichoptera pupae exuviae	
		Mites adult	
		Bivalvia	
		Gastropoda	
		Nematoda	
		Collector bag	
	Other TFS	Ephemeroptera adult	
		Plecoptera adult	
		Trichoptera adult	
		Araneae	
		Coleoptera larvae	
		Lepidoptera larvae	
		Lepidoptera adult	
		Oligochaeta	
		Down feather	
Excluded items:	Sand grains		
	Algae		
	Plant fragments	Moss	
	Salmon egg	Roots	
	extra Wings	Seeds	
	Invertebrate eggs	Lichens	
	Unidentified pupa	Plant stems, and shoots	
	Unidentified larvae		
	Unidentified		

3. Key for the correlation net.

Variables	Correlation net	Streams				
		SFC	WPC	IVS	BBS	RPC
Age	N1	39	65	141	181	206
Area (km^2)	N2	13,11	29,68	19,04	22,44	20,14
Perimeter (km)	N3	19,79	38,63	26,06	30,33	26,17
Compactness	N4	1,54	2,00	1,68	1,81	1,64
Relief (m)	N5	705,91	1235,13	947,96	738,27	774,45
Area < 50m km^2	N6	3,37	2,86	1,05	2,12	4,17
%Waterbodies in the watershed	N7	5,63	4,99	0,02	0,44	0,13
%Vegetation in the watershed	N8	72,43	50,62	70,23	71,97	77,21
Stream order	N9	3	3	4	4	4
Total number of streams (Nu)	N10	29	32	38	38	49
Total stream length (km)	N11	21,67	34,61	26,94	34,11	32,40
Drainage density	N12	1,66	1,17	1,42	1,53	1,61
Stream.freq. (n)	N13	2,22	1,08	2,01	1,70	2,43
First Order streams length (km)	N14	12,24	17,70	15,28	14,26	17,39
Mean Bifurcation ratio (Rb)	N15	4,80	5,38	3,17	3,17	3,59
Length ratio (Rl)	N16	2,66	3,20	3,18	3,62	2,60
Hack main channel (km)	N17	6,14	11,84	9,47	9,55	9,73
Hack mean main channel slope	N18	0,09	0,06	0,06	0,06	0,06
Hack mean Main channel gradient	N19	0,08	0,05	0,05	0,04	0,04
Hack mean Main channel elevation diff.	N20	501,12	585,24	507,95	389,84	376,71
Main channel sinuosity	N21	1,67	1,34	1,74	1,68	1,56
Main channel azimuth	N22	203,81	95,18	85,93	21,02	58,19
Basin length (km) (Lb)	N23	6,42	13,25	10,20	10,42	10,48
Max watershed slope in degrees	N24	63,90	73,63	74,24	69,85	69,06
Mean watershed slope in degrees	N25	16,09	21,78	20,84	18,08	17,45
Median watershed slope Degrees	N26	13,63	20,68	20,81	16,44	15,11
Mean watershed elevation (m)	N27	214,08	357,25	314,28	228,82	232,80
Median watershed elevation	N28	94,18	291,71	271,47	203,58	188,86
Melton ruggedness number	N29	0,19	0,23	0,22	0,16	0,17
Relief Ratio (Rhl)	N30	110,46	93,53	93,18	71,29	73,93
Form Factor Ratio (Rf)	N31	0,32	0,17	0,18	0,21	0,18
Elongation Ratio (Re)	N32	0,64	0,46	0,48	0,51	0,48
Length Area Relation	N33	6,56	10,71	8,20	9,05	8,48
Fitness Ratio (Rf)	N34	1,09	0,90	1,03	1,12	1,24
Length of overland flow (Lo)	N35	0,30	0,43	0,35	0,33	0,31
Constant of channel maintenance	N36	0,60	0,85	0,70	0,65	0,62
Circulatory Ratio (Rc)	N37	0,42	0,25	0,35	0,31	0,37
Rho	N38	0,55	0,60	1,00	1,14	0,72
Mean pink counts	N39	746	8193	288	1558	747
Mean $\delta^{15}N$	N40	0,56	2,08	-0,02	3,10	2,05
Mean $\delta^{13}C$	N41	-27,35	-27,09	-29,09	-31,21	-30,80
Mean %N	N42	8,70	8,55	8,64	8,58	8,88
Mean %C	N43	42,78	42,98	42,68	41,51	43,10
Mean C/N Ratio	N44	9,73	8,80	9,30	9,01	10,35
$\delta^{13}C$ SD	N45	1,45	1,80	2,98	4,05	4,17
$\delta^{15}N$ SD	N46	3,40	2,89	3,73	3,76	4,00
%N SD	N47	5,14	4,89	5,10	5,12	5,22
%C SD	N48	11,77	11,44	13,17	12,69	11,83
$\delta^{13}C$ Range	N49	6,64	6,86	10,32	13,48	14,29
$\delta^{15}N$ Range	N50	11,97	10,28	12,88	11,23	11,88
%C Range	N51	44,93	43,76	48,00	47,44	47,36
%N Range	N52	14,30	14,28	14,58	14,51	14,34
Mean FL juvenile coho salmon	N53	72,03	70,88	66,18	63,70	69,96
Mean FL juvenile Dolly Varden	N54	97,58	111,95	102,34	80,03	81,30
Mean CPUE juvenile coho salmon	N55	11,81	8,38	3,13	5,30	11,73
Mean CPUE juvenile Dolly Varden	N56	2,83	2,45	2,13	1,13	5,19
Mean salinity at 1m	N57	15,89	16,54	22,27	26,52	29,31
% AFS juvenile coho salmon	N58	83,17	91,32	66,35	77,92	85,81
%TFS juvenile coho salmon	N59	16,79	6,21	33,55	17,33	11,91
%MFS juvenile coho salmon	N60	0,04	2,47	0,09	4,74	2,29
%AFS juvenile Dolly Varden	N61	95,21	95,66	98,18	83,03	91,91
%TFS juvenile Dolly Varden	N62	4,76	0,80	1,82	8,63	2,28
%MFS juvenile Dolly Varden	N63	0,03	3,53	0,00	8,33	5,81
%AFS Utilization juvenile coho salmon	N64	98,88	97,62	95,56	93,90	96,70
%TFS Utilization juvenile coho salmon	N65	76,40	46,43	85,56	80,49	64,84
%MFS Utilization juvenile coho salmon	N66	1,12	16,67	2,22	31,71	23,08
%AFS Utilization juvenile Dolly Varden	N67	91,01	97,83	92,98	85,42	93,33
%TFS Utilization juvenile Dolly Varden	N68	44,94	19,57	31,58	33,33	11,11
%MFS Utilization juvenile Dolly Varden	N69	1,12	36,96	0,00	35,42	21,11
Niche breadth juvenile coho salmon	N70	0,54	0,41	0,57	0,52	0,44
Niche breadth juvenile Dolly Varden	N71	0,43	0,31	0,35	0,39	0,24
Morisitas overlap index	N72	0,81	0,91	0,77	0,56	0,82
Mean FL pumped juvenile coho salmon	N73	74,57	76,68	66,07	70,78	75,84
Mean FL pumped juvenile Dolly Varden	N74	99,10	116,41	110,12	82,88	84,13
Empty gut per juvenile coho salmon	N75	0,00	0,02	0,02	0,04	0,02
Empty gut per juvenile Dolly Varden	N76	0,09	0,02	0,07	0,15	0,07
%AFS per juvenile coho salmon	N77	0,81	0,90	0,67	0,67	0,81
%TFS per juvenile coho salmon	N78	0,19	0,06	0,31	0,21	0,14
%MFS per juvenile coho salmon	N79	0,00	0,02	0,00	0,08	0,03